FUNCTION, FORM, AND RECOGNITION OF THE SONGS OF GOLDEN-WINGED WARBLERS (*Vermivora chrysoptera*) AND BLUE-WINGED (*V. pinus*) WARBLERS

A Dissertation Presented by

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ABSTRACT

FUNCTION, FORM, AND RECOGNITION OF THE SONGS OF GOLDEN-WINGED (*Vermivora chrysoptera*) AND BLUE-WINGED (*V. pinus*) WARBLERS

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I studied the relationship between the form of vocal displays and functional aspects of their use in two species of hybridizing North American wood warblers (Parulinae). Both Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) have a simple song system in which each male has a repertoire of two stereotyped songs, type I and type II. Observations of territorial male Golden-wings show that long type I songs, short type I songs, and type II songs are used as a graded series during actual and simulated agonistic encounters. The amount of long type I singing, but not of short type I or type II singing, decreases upon attraction of a mate, and males were observed to sing only type I songs when consorting with females. These patterns of use support the view that

type I songs in this species have special intersexual (mate attraction) functions and that type II songs have special intrasexual (territorial) functions.

Analysis of song samples from throughout the ranges of both species reveals dramatic differences in the form of the two song types. The structure of type I songs is stereotyped both micro- and macro-geographically and is highly species-specific. Type II songs display marked geographic variation and may show little species-specificity in areas of sympatry. Despite infrequent but continuous hybridization in the two species, no divergence between the mate attraction songs (type I) was detectable.

Two-speaker playback experiments on song discrimination were performed in an allopatric Golden-wing population in Minnesota and a predominantly Blue-wing population in Massachusetts. Males at both locations discriminated readily between normal conspecific and heterospecific type I songs, but response to songs was affected by experimental manipulations of species typical song pattern and frequency characteristics. Golden-wings displayed an ability to differentiate between type I song components using information about frequency and amplitude modulation. Responses to experiments with type II songs show that Golden-wings may orient more closely to familiar type II songs than to unfamiliar conspecific or heterospecific songs.

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CHAPTER 1

INTRODUCTION

The study of the behavioral relationships of closely related species is a particularly rewarding endeavor in modern biology. Documenting differences between congeners in behaviors related to communication, reproduction, and foraging informs our knowledge of the functional aspects of behavior and furthers our understanding of the evolutionary and developmental processes that gave rise to them. Particularly when interactions between species are sustained and lead to interspecific aggression and/or hybridization, the study of behavior may stimulate new ideas in ecology and taxonomy.

The complicated relationship between Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) has interested biologists for over a century. Ornithologists in the late 1800's were puzzled by the appearance of two rare birds, the Brewster's and Lawrence's Warblers, that seemed to combine the familiar and distinctive plumage characteristics of Golden-wings and Blue-wings. Observers were impressed by the fact that these unusual forms generally sang a song typical of one of the common species, but were confused by occasional observations of what appeared to be a normal Golden-wing or Blue-wing singing the other species' song. The mystery was clarified with the publication of Walter Faxon's (1913) careful observations of the nest and young of a Golden-wing male and a Blue-wing female in Lexington, Massachusetts. The progeny of this mixed species pair grew into adult Brewster's Warblers.

Since that time, Golden-wings and Blue-wings have become one of the best studied examples of avian hybridization. Although historically the ranges of these species were probably completely separate, Blue-wings are now expanding widely into areas formerly occupied exclusively by Golden-wings (Short 1963, Gill 1980, Will 1986). Interbreeding occurs in areas of recent contact, despite pronounced differences in plumage color and pattern. The result is a small but apparently enduring number of viable hybrids with a continuum of plumage types and an often puzzling mismatch of plumage type and vocal behavior (Ficken and Ficken 1967, Murray and Gill 1972).

Although the first modern studies of these species concentrated on the genetics of hybridization (Parkes 1951, Short 1963), ornithologists soon realized the opportunity to investigate a variety of behavioral and ecological phenomena. Questions about the causes of hybridization stimulated field work on the habitat and foraging preferences of the two species (Ficken and Ficken 1968c, Confer and Knapp 1981) and on the apparent lack of interspecific territoriality (Ficken and Ficken 1968b, Murray and Gill 1972, Will 1986). Other studies documented similarities in courtship (Ficken and Ficken 1968a) and singing behavior (Ficken and Ficken 1967, Gill and Murray 1972a). A debate arose concerning the existence of effective reproductive isolating mechanisms between the two species (Ficken and Ficken 1968d, Short 1969), which in turn stimulated a number of experimental investigations of the role of song in species discrimination (Gill and Lanyon 1964, Ficken and Ficken 1969, Gill and Murray 1972b, Crook 1984).

The present work builds upon the foundation laid by these previous studies. My primary aim has been to investigate the relationships between the form of vocal signals in these species and the functions they fulfill, including a determination of how signal form affects the recognition of species-specific songs. Compared to songbirds

in general, and to other wood-warblers (parulines) in particular, the vocal repertoires of these species are both simple and quite similar to each other. This apparent simplicity has several benefits for the field biologist: it facilitates field study, it enables detailed comparisons of vocal behavior between the two species, and it allows the examination in simpler form of singing behaviors that are less tractable in species with larger, more complex repertoires.

Any study of an animal's visual or vocal displays must begin with a detailed description of the displays themselves and the circumstances in which they are used. Despite the numerous published accounts of courtship and territorial behavior in these species (Baird 1967; Ficken and Ficken 1968a, b; Meyerriecks and Baird 1968; Murray and Gill 1976), the bulk of information concerning songs has been anecdotal in nature. Only two studies (Ficken and Ficken 1967, Kroodsma 1988), both of which suggested a functional dichotomy in the use of the two song types, have attempted a more systematic approach. I present in Chapter 2 the results of an extensive study of the singing behavior of an historically allopatric population of Golden-winged Warblers in north-central Minnesota. I show that the vocal behavior of Golden-wing males is organized around the association of song types and specific singing behaviors, add substantially to the detail of our understanding of the functional use of song types, and describe a previously unreported flight song display.

Previous descriptions of Golden-wing and Blue-wing songs were based on comparisons of gross song morphology from a relatively limited geographic sampling, but suggested interesting correlations of the degree of variability in song form with song function (Lanyon and Gill 1964, Kroodsma 1981) and with the extent of species range overlap (Gill and Murray 1972a). In Chapter 3, I report the results of a detailed analysis of songs from a wide range of locations throughout the ranges of both species. I quantified both the gross characteristics of songs and the fine structure of

song components. Patterns of song variation both within and between species are discussed and interpreted in the light of my findings on the extent of geographic variation in each song type.

The apparent similarities of Golden-wing and Blue-wing vocalizations led to a number of experimental investigations of whether these songs function as species-specific characters (Gill and Lanyon 1964, Ficken and Ficken 1969, Gill and Murray 1972b, Crook 1984). In general, the results showed that males were able to discriminate between each species' songs, but responses seemed to depend on which song type is used as a stimulus. My own experiments, presented in Chapter 4, were designed to reveal exactly what parameters of type I songs, or combinations thereof, males use in discrimination, and whether responses to type II songs are based on familiarity with local songs or on perception of species-specific differences.

CHAPTER 2

THE SINGING BEHAVIOR OF GOLDEN-WINGED WARBLERS

Unlike those songbirds that appear to use a variety of songs interchangeably, many wood warblers (Parulinae) have a repertoire of song types that are used in different ways in different contexts. In some warblers, the contexts in which songs are used suggest that song types are functionally distinct and carry predominantly inter-sexual (mate attraction) or intra-sexual (territorial) messages (Chestnut-sided Warbler [*Dendroica pensylvanica*], Yellow Warbler [*D. petechia*], and American Redstart [*Setophaga ruticilla*], Ficken and Ficken 1965; Golden-winged Warbler [*Vermivora chrysoptera*] and Blue-winged Warbler [*V. pinus*], Ficken and Ficken 1967, Kroodsma 1981; Black-throated Green Warbler [*D. virens*], Morse 1970; and Grace's Warbler [*D. graciae*], Staicer 1982). In addition, observations of some species reveal that certain song types, or groups of song types, may be associated with distinct singing behaviors characterized by, for example, differences in rate of delivery or in sequential variety (Grace's Warbler, Staicer 1982; American Redstart, Lemon et al. 1985).

Golden-winged and Blue-winged warblers have a simple song system in which each male has a repertoire of two stereotyped songs, type I and type II (Lanyon and Gill 1964). An extensive literature, often with an emphasis on the role of vocalizations, documents within- and between-species behavioral interactions in this frequently hybridizing species pair (Gill and Lanyon 1964; Ficken and Ficken 1967, 1968a, b, 1969, 1973; Baird 1967; Meyerriecks and Baird 1968; Gill and Murray 1972b; Murray and Gill 1976). Despite this emphasis, only a very general

picture of singing behavior has emerged; most authors note only that type I is the most frequently used song and that type II is restricted to particular situations. Only two studies attempt a more detailed analysis of patterns of song use. Ficken and Ficken (1967) found that levels of type I song activity are greater in unmated than in mated males of both species and that type II song is given most commonly during encounters with other males, suggesting mate attraction (type I) and territorial (type II) functions. Kroodsma (1988) provides a brief description of Blue-winged Warbler song use that is consistent with the view that different singing behaviors are used with the two song types.

I here present a comprehensive description of singing behavior in a population of Golden-winged Warblers that is currently and historically allopatric with Blue-winged Warblers. Through a series of early morning observations and song playback experiments, I investigated differences in the use of songs based on the behavioral context and on the time of day and season, and whether specific singing behaviors were associated with each song type.

Methods

I studied Golden-winged Warblers in the Itasca State Park area, Hubbard and Clearwater Counties, of north-central Minnesota during May and June 1984-1986. Although Blue-winged Warblers nest only 300 km to the southeast, only one Blue-winged Warbler and one female hybrid have been reported from the area, both in 1986 (Highsmith 1987). Except for these individuals, the Itasca population appears phenotypically pure and shows no signs of genetic introgression with Blue-winged Warblers (Gill 1987). I performed all observations and experiments on active

Golden-winged Warbler territories between 04:30 and 13:00 h CDT, with the help of several field assistants.

Song Description

Type I song (Fig. 2.1a, p. 22) normally consists of a high frequency buzzy phrase followed by one to six buzzy phrases of lower frequency. Type I song length is referred to by the number of times each phrase type occurs in a song; a song with a single high frequency phrase followed by three lower frequency phrases, for example, is a 1-3. Based on observations of song use by undisturbed males, I usually consider type I songs with four or more total phrases to be long type I songs, and songs with three or fewer total phrases to be short type I songs (see Results). Type II song (Fig. 2.1b) contains three to five syllable types and ends with a terminal buzzy phrase.

Observations of Singing Behavior

Although the singing behavior of over 15 different males was observed, I here report data from the six color-banded males that were observed most intensively. Because previous accounts of Golden-winged Warbler singing behavior did not cover the early morning period, my assistants and I usually arrived on territories between 04:30 and 05:00 h to begin our observations before males started their singing activity each day. Males A, B, and C (1986), D and E (1985), and F (1984) were monitored continuously from the beginning of song activity to well after sunrise, and at various times later in the day. We used binoculars, stop watches, and data sheets, marked in minutes and seconds, to record the following: song type; song length; whether songs were loud or muted; the male's position on the territory; and the behavioral context of a male's singing, including any interactions with conspecifics.

The data from males A, B, and D that were used to compare singing behavior during the pair formation period were limited to those that were collected between the

start of singing activity and 06:30 over the birds' first nineteen days on territory. I determined singing rate by counting the number of songs in each bout of continuous singing and dividing by the number of minutes of continuous song. I express the amount of type II song activity as the duration in minutes of the essentially continuous early morning type II bout, measured from the first type II song of the day to the last type II song given before the switch to pure type I singing. Because type I songs are sung more intermittently, the amount of type I song activity is best expressed as songs per minute of observation. Multiple linear regression analysis of male A's singing behavior was done using the Interactive Data Analysis Package (Wiedmann and Hosmer 1983).

Song Playback Experiments

We noted responses to simulated territorial intrusions during the course of song playback experiments on species discrimination with over 250 different males. Pairs of song stimuli were played at a natural singing rate from two speakers placed on a male's territory. Each playback experiment consisted of five periods: 5 minutes of pre-playback observation, 5 minutes of stimulus presentation, a 3 minute silent intermission, 5 minutes of stimulus presentation, and 5 minutes of post-playback observation. Males were scored on the basis of whether they sang any type I or type II songs during each period, and on the length of type I songs sung. If an individual sang both song types during a particular period, it was scored for both.

We used Uher 4200 or 4400 Report Monitor tape recorders and Olympus SP5 speakers (modified by Mineroff Electronics) to broadcast songs. Type II song stimuli (total of 8 different experimental tapes) consisted of natural Golden-winged and Blue-winged Warbler type II songs. Type I song stimuli (total of 25 different experimental tapes) included various combinations of natural Golden-winged Warbler type I, natural Blue-winged Warbler type I, and artificial type I songs composed of

elements from both species. Some males also heard several type I songs during pre-playback or intermission from a separate tape used to attract males to the playback area. A small number of males received both a type I and a type II playback, but otherwise a male was used only once. Vocal responses of males to playbacks containing only natural or only artificial type I songs did not appear to differ, so all type I playbacks were lumped for analysis. Results from type I and type II playback experiments were analyzed separately. Statistical comparisons of changes in singing behavior between experimental periods were made using McNemar's test for significance of difference between two correlated proportions (two-tailed, Ferguson 1976).

Results

Daily Patterns of Singing Behavior

Undisturbed, mated Golden-winged Warbler males exhibited two distinct modes of singing behavior that were characterized by differences in song type and time of day.

Type II Singing Behavior. Except for very early in the season, males began each day's singing activity with an extended and rapidly paced bout of type II songs. Many males began the bout from the same perch each day and sang continuously for 30-40 min, stopping around sunrise. Typically a male sat mid-level or high in a shrub or tree, often at an edge of his territory closest to conspecific neighbors with whom he counter-sang. Males frequently made short-distance perch changes.

Although most males began the bout with complete songs, others sang only the first two or three syllable types of their normal type II song for several minutes, and only gradually lengthened these songs to include the terminal buzz. Chip notes, similar in structure to the initial type II syllables, were used frequently between

songs. Songs were delivered at a rapid rate throughout the bout although the rate differed greatly both among males (mean = 8.8 $\pm$ 2.2 [SD] songs/min, N = 5 males) and within individuals (Table 2.1, p. 20). Male E, for example, was once observed singing at the unusually high rate of 18-20 songs/min for a two minute period.

Interruptions of the type II bout were not uncommon but their causes were difficult to observe because of low light levels and thick vegetation. Males sometimes paused to chase intruding males or to accompany females. In both cases, males and females uttered a low, buzzy "zzt", either singly or repeated in slow chatter-like strings. Following such disturbances, males typically returned to the same or a different perch and resumed type II singing.

Flight song displays can be given at any point in the type II bout, but five of the eleven males in which I observed it used it frequently as one of their very first songs of the morning. To perform the display a male flew up in an arching path, flapped his wings stiffly, gave the song at the peak of his ascent, and flapped or glided down to the same or a different perch (similar to description for other parulines in Ficken and Ficken 1962). The song itself was a modified version of the male's type II song, differing in the addition of two or three syllable types to the beginning of the song (Fig. 2.1c). I was able to obtain good recordings from only two males, but the structure of the syllables peculiar to the flight songs was similar in each individual. I frequently observed one to three flight song displays during a male's early morning type II bout, but on some days I heard none at all. The most I observed during a single bout was a total of nine given by male A in a 30 min period on 23 May 1986. Flight song displays were noted as early in the season as 17 May and as late as 20 June.

A male's early morning type II bout ended with a minute of intermingled type I and II songs, an abrupt switch to type I songs, or a cessation of singing activity.

Type II songs were often used later in the morning, but with several notable differences. Rather than forming a distinct bout, strings of type II songs were likely to be mixed with strings of type I, usually preceding or following an interaction with another male. Although song rate remained high and some males sang incomplete songs, flight song displays were not used, chipping between songs was less frequent (although the "zzt" note was sometimes used), and males often sang at reduced volume.

Type I Singing Behavior. Whether a male's first type I songs of the day were continuous with the end of his type II bout, or whether he stopped and began later in the morning, type I singing was characterized by a lower mean song rate (3.9 ± 0.6 [SD] songs/min, N = 5 males), lack of chip notes between songs, and absence of flight song displays. Relatively little variation existed in type I song delivery rates among males (Table 2.1); even during counter-singing the highest type I rate I observed was 8 songs/min, again from male E.

There was variation among males in the length of type I songs included in their individual repertoires. Individuals generally had a "preferred" type I rendition that was their most common song in bouts of undisturbed singing. This song was usually the longest or next longest type I song in a male's repertoire and contrasted with the shorter songs that a male sang during territorial disputes (see below). The "preferred" song for most males was a 1-3 (Fig. 2.1a), but I encountered a small number of males who sang predominantly 1-2's and another who sang predominantly 1-4's. Male A is typical of 1-3 singers; 57% of all songs observed over two seasons were 1-3's and less than 1% were 1-4's or longer. All of the six males that I intensively observed "preferred" 1-3's, except for male D, who sang mostly 1-2's (85% were 1-2's, only 3% were 1-3's).

There was no distinct type I bout, analogous to the type II bout, that was predictable in time and place. Although an unmated male sometimes sang type I for hours from a single exposed perch, mated males were more likely to sing intermittently from a succession of perches around the perimeter of their territory, or not to sing at all for long periods. I have observed undisturbed males singing type I while preening or foraging, and from perches in thick vegetation where they were mostly obscured from view. Type II singing, at least during the pre-dawn bout, appeared to preclude preening or foraging, perhaps because of low light levels.

Seasonal Patterns of Singing Behavior

Type II Singing Behavior. Analysis of samples from four males over the first nineteen days after their arrival on territory showed that the duration of the early morning type II bout tended to increase throughout this period (Fig. 2.2, p. 23). Males did not begin singing these type II bouts until two to four days after arrival, and bouts were likely to be quite short (less than 15 minutes) for the first ten days or so. Some bouts eventually increased to 45 min in length as males began singing earlier before sunrise.

Type I Singing Behavior. Type I singing activity decreased over the course of the breeding season. Following an abrupt drop from almost constant type I singing before males were paired in May, type I singing decreased more gradually until, by mid to late June, songs were quite sporadic. Early in the season, before type II bouts were established, some males began their daily singing before sunrise with type I songs. In these instances, singing rate and behavior were the same as in typical later morning type I singing.

Social Patterns of Singing Behavior

Singing Behavior During Song Playback Experiments. Males used both their type I and type II singing behaviors during simulated territorial intrusions provided

by song playback experiments. The most striking change in song type use occurred during the first stimulus presentation period, regardless of whether the experimental songs were type I or type II (Fig. 2.3, p. 24). Although the number of males singing type I songs decreased slightly from the pre-playback to the first stimulus period, the number singing type II songs increased significantly. The same general pattern was evident over all five experimental periods: the number of males singing type II increased during periods of stimulus presentation and decreased during periods of silence, while the number of males singing type I decreased during stimulus periods and increased when the stimulus was withdrawn. These results agree with other playback experiments and observations of males in actual territorial encounters (Ficken and Ficken 1967, 1968b, 1969, 1973; Highsmith, pers. obs.). Responses to the playback experiments also showed that there was an overall increase in singing activity, in that more males were vocalizing after the experiments than before.

A pattern was also evident in the length of type I songs used by males during playback experiments (Fig. 2.4, p. 25). Although the numbers of males singing short and long type I songs was approximately equal just before both type I and type II experiments, the number of males singing short songs increased significantly, and those singing long songs decreased significantly, during the first stimulus period. Singers of short songs outnumbered singers of long songs throughout all but the pre-playback period.

Singing behavior during mate attraction and pair formation. My assistants and I were able to follow three Golden-winged Warbler males through the process of mate attraction and pair formation. All three males engaged in a variety of visual courtship displays, which are well documented elsewhere (Ficken and Ficken 1968a, Baird 1967). Two of the males, B and D, successfully attracted and paired with single females. Male A, on the other hand, provided a natural mate-loss experiment.

Male A's first potential mate, a female Blue-winged Warbler, remained on his territory for only three days, during which time she was closely attended by male A and appeared to prospect for nest sites. After her disappearance, male A remained unpaired for five to seven days until he finally attracted a Golden-winged Warbler female. Although male A's circumstances were unusual in this study population, I believe his behavior may be considered representative of a normal Golden-winged Warbler male. Interspecific pairing of Golden-winged and Blue-winged Warblers is not uncommon in areas of more extensive sympatry and, except for song morphology, courtship displays of the two species are essentially identical (Ficken and Ficken 1968a). Also, male A's behavior with the two females did not differ in any notable way, nor did it differ from that of the other two males under observation.

The presence of a female on a male's territory had no consistent effect on the type II singing behavior of the three males during pair formation. Male A sang progressively longer type II bouts throughout this period (Fig. 2.2). Analysis by multiple linear regression showed that the number of days since he arrived on territory contributed significantly to explaining variation in the amount of his type II singing ($t = 6.89$, $P = 0.0001$), but female presence did not ($t = 0.86$, $P = 0.41$; female presence and days together: $F = 25.3$, $df = 2, 7$, $R^2 = 0.88$, $P = 0.0006$). Male B (Fig. 2.2) showed a smaller increase in type II bout length before and after female arrival, and male D's bouts decreased in length the first two days on which he was closely attending his female. Males appeared to cut short or abandon their type II bouts in order to closely attend the females on some days, but I never observed males to sing type II while in close association with females.

All three males showed a dramatic change in long type I singing activity with the arrival of the female. In general, males sang extended, uninterrupted bouts of long type I songs before attracting a female, but sang very few long type I's once a

female was present. For male A (Fig. 2.5, p. 27), long type I activity decreased with the arrival of the Blue-winged Warbler female, rose when she disappeared, and fell off again with the arrival of the Golden-winged Warbler female. Regression showed that female presence contributed significantly ($t = -4.09$, $P = 0.003$) to explaining variation in the amount of his long type I singing, but number of days on territory did not ($t = -0.217$, $P = 0.83$; female presence and days together: $F = 7.43$, $df = 2, 7$, $R^2 = 0.68$, $P = 0.018$). Males B and D (Fig. 2.5) also showed a sharp drop in the amount of their long type I activity immediately after attracting females.

Males showed no corresponding variation in the amount of their short type I singing, although they did use sporadic, usually muted, short type I songs when close to a female. The amount of short type I activity varied little before and after female arrival for male A (Fig. 2.5; female presence: $t = 0.136$, $P = 0.89$; number of days on territory: $t = -0.590$, $P = 0.57$; female presence and days together: $F = 0.177$, $df = 2, 7$, $R^2 = 0.04$, $P = 0.84$) and for male D (Fig. 2.5). Male B's short type I singing did increase on the first day of his female's presence, but returned to previous levels the following three days (Fig. 2.5).

Discussion

My results generally support the descriptions of Golden-winged Warbler singing behavior made by Ficken and Ficken (1967) but provide a more complete picture of the ways in which males use their two song types. Although previously considered an infrequently used song, type II song constitutes a substantial part of a male's vocal behavior and is not limited to use during conflicts between males. Except at the very beginning of the season, type II makes up a distinct and lengthy bout of songs, performed daily at the same time and place, that initiates a male's daily

singing activity. Especially late in the season, when most mated males are singing type I only sporadically, the early morning type II bout may be the only predictable element of a male's singing behavior on a particular day.

Singing in flight has been noted in a number of *Vermivora* (Bent 1953, pp. 42, 84; Pitelka 1939; Ficken and Ficken 1962; Gilbert 1983), but modification of both the song and pattern of flight has been previously reported only in the Nashville Warbler (*V. ruficapilla*, Bowles and Bowles 1906, Chapman 1907). Golden-winged Warblers occasionally sing normal type II songs in flight, especially during song playback experiments, but their flight song display is distinctly different. The range of dates and time of day of my observations do not strongly support the suggestion that these displays are primarily given late in the day and late in the season (Ficken and Ficken 1962). I observed all but one of more than 30 displays during the early morning type II bout, and the other one around 07:00 h. Although I have not made extensive observations in the evening, others have noted flight song displays during a brief type II bout at that time (T. Will pers. comm.).

Both observational and experimental data show that a male's song repertoire exists as a graded series. A male sings long type I songs when he is relatively undisturbed, and shortens these when presented with either a real or simulated male intruder (Fig. 2.4), or when closely accompanying a female. If an interaction with another male escalates, males switch to type II songs, although I never observed males to use type II songs when in close contact with females. Responses to song playback show that males often switch songs in stepwise fashion, up or down the series (eg. 1-3 to 1-1 to type II), but they may also switch directly from long type I to type II or vice versa. Ficken and Ficken (1967) obtained similar results for Golden-winged Warblers from a population sympatric with Blue-winged Warblers in New York.

This pattern of song use resembles the "motivational continuum" Lein (1972) has proposed to explain the use of song types by Black-throated Green Warblers. Territorial Black-throated Green Warbler males, Lein suggests, spontaneously produce type B songs when undisturbed, but switch to type A in the presence of a variety of external stimuli including other males, low light levels, or proximity to the territory boundary (but see Morse 1970). Similarly, Chestnut-sided Warblers (Lein 1978) switch up or down within a series of accented and unaccented ending song types depending on the singer's "mood," location on his territory, and the likelihood of a dispute with a neighbor. Lein argued that song in these and other warbler species functions primarily in territorial establishment and defense. While he notes that the message a song type carries may well have different meanings for male and female conspecifics, he concludes that any inter-sexual function of song is supplementary to the intra-sexual (Lein 1978). Although song use by Golden-winged Warblers appears consistent with Lein's "motivational continuum," observations of the contexts in which songs are used do not support his functional explanation. There appears to be a major functional distinction between the two extremes of the graded series, type II songs and long type I songs.

Patterns of song use by Golden-winged Warblers early in the season suggest that long type I songs, but not short type I or type II, are particularly important in mate attraction. The early morning type II bout is absent, or of short duration, during this period (Fig. 2.2), although type II is used during encounters with other males at that time. The presence of a female on a male's territory had no consistent effect on the amount of short type I (Fig. 2.5) or type II singing. In contrast, female presence correlated strongly with a sharp drop in long type I singing activity, and one male who lost his first mate reverted to a high level of long type I activity until he attracted another (Fig. 2.5). Further, although both song types are used in agonistic

situations, songs from the middle of the graded series (short type I) are used with conspecifics of either sex; daytime type II songs appear to be reserved for use during interactions with other males.

The data thus support the general view that type I and type II songs carry inter- and intrasexual messages, respectively (Ficken and Ficken 1967, Kroodsma 1981), but with two important qualifications. First, the mate attraction function appears limited to a male's long type I song. Second, each song type has a specific, but not a solitary, message: despite type I song's special mate attraction function, it is also used by males in territorial disputes, and despite type II's special territorial function, it may also carry information about species or individual identity that is available to listening females.

Differences between type I and II songs are further underlined by the distinctive behaviors associated with the delivery of each song type. Type I and type II singing behaviors differ in song rate, use of chip notes between songs, use during flight displays, and use during well defined, ritualized song bouts. It is likely that Blue-winged Warblers share many of the patterns of behavior, if not specific behaviors, that I have described for Golden-winged Warblers. Blue-winged Warbler males sing an early morning type II bout and singing rates of type I and type II songs differ in ways parallel to those of Golden-winged Warblers (mean rate of type I songs = 4.6 $\pm$ 0.8 [SD] songs/min, mean rate of type II songs = 11.9 $\pm$ 1.7 [SD] songs/min, N = 5 Massachusetts Blue-winged Warbler males). There is also evidence that modified type II songs are used in a flight display (pers. obs.; Kroodsma, unpublished data).

This correlation of particular behaviors and particular song types is also seen in some parulines with much larger, more complex repertoires. Species may sing specific song types, or groups of song types, with consistent differences in rate or

pattern of delivery. Male American Redstarts (mean repertoire size = 4.4 songs per adult male), for example, consistently repeat one of their song types over and over (repeat mode) but sing the others with high immediate variety (serial mode) (Lemon et al. 1985). For Grace's Warblers, who typically have repertoire sizes of six or more song types per male (Staicer 1982), similarities with Golden-winged Warblers are pronounced both in how the songs are sung and in what contexts they are used. Group A songs, used prior to pairing and in the presence of females, are sung with low or no sequential variety and at a slow rate. Group B songs, used primarily during an early morning bout and in interactions with other males, are sung with immediate variety and at a high rate (Staicer 1982).

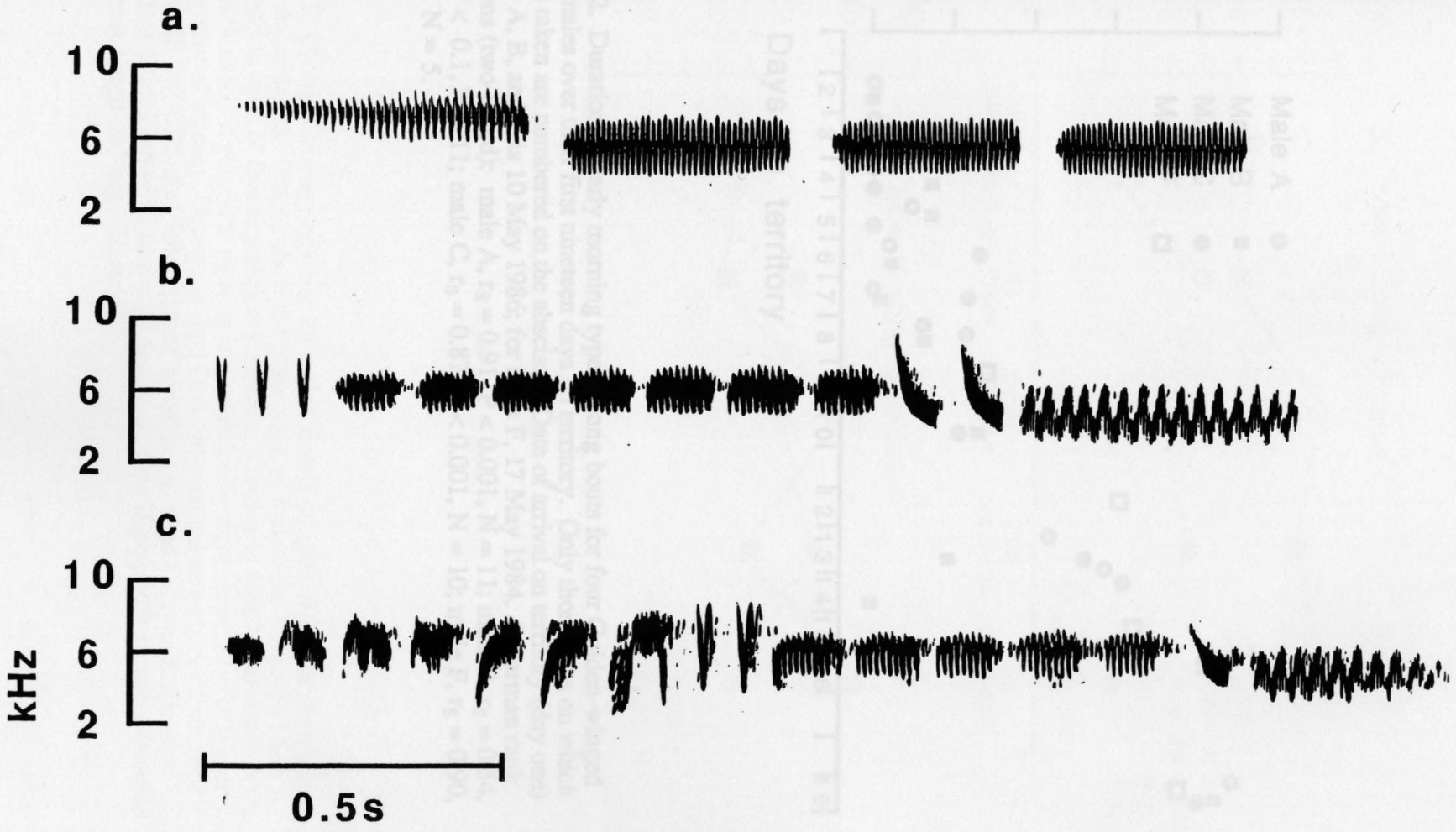
These comparisons among warbler species suggest that the complexity of singing behavior may depend as much on how the repertoire is used as it does on repertoire size. Despite the limitation of two stereotyped song types per male, the flexibility of Golden-winged Warbler singing behavior serves to create a larger effective repertoire. Golden-winged Warbler males use songs as a continuous series and as discrete song types. Distinctions between mate attraction and agonistic functions are apparent both between the two song types and within a single song type (type I).

Table 2.1. Mean singing rates of type I and type II songs in songs/min.

Male	type I	type II
A	3.9 ± 1.4 (10)[a]	6.5 ± 1.4 (7)[a]
B	3.7 ± 0.5 (6)	6.5 ± 1.9 (7)
D	4.3 ± 1.4 (5)	10.4 ± 1.6 (6)
E	4.5 ± 0.6 (6)	10.0 ± 1.9 (2)
F	3.2 ± 0.3 (6)	10.8 ± 2.6 (6)

[a] mean ± SD (number of song bouts used to calculate mean)

Figure 2.1. Song repertoire of Golden-winged Warbler male A. Sonagrams were prepared on a Kay Elemetrics Co. Model 7029A Sonagraph (600 Hz filter). a. type I song. b. type II song. c. modified type II song used in flight song display.


a.
10
6
2
b.
10
6
2
c.
10
6
2
kHz
0.5s

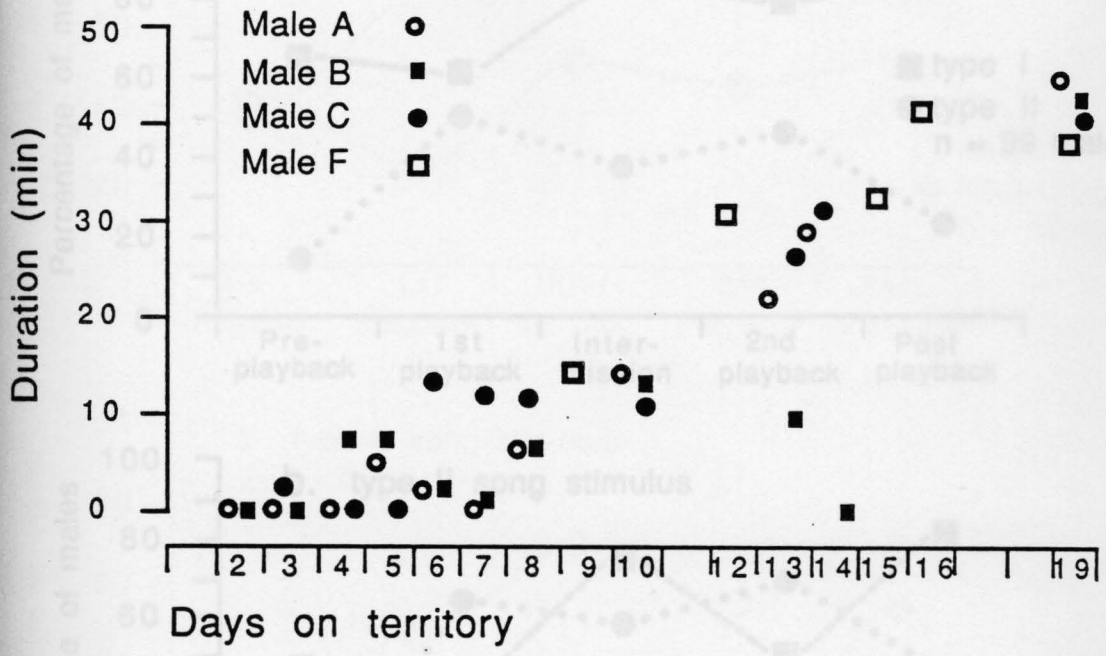


Figure 2.2. Duration of early morning type II song bouts for four Golden-winged Warbler males over their first nineteen days on territory. Only those days on which data were taken are numbered on the abscissa. Date of arrival on territory (day one) for males A, B, and C is 10 May 1986; for male F, 17 May 1984. Spearman rank correlations (two-tailed): male A, $r_S = 0.91$, $P < 0.001$, $N = 11$; male B, $r_S = 0.54$, $0.05 < P < 0.1$, $N = 11$; male C, $r_S = 0.87$, $P < 0.001$, $N = 10$; male F, $r_S = 0.90$, $P = 0.05$, $N = 5$.

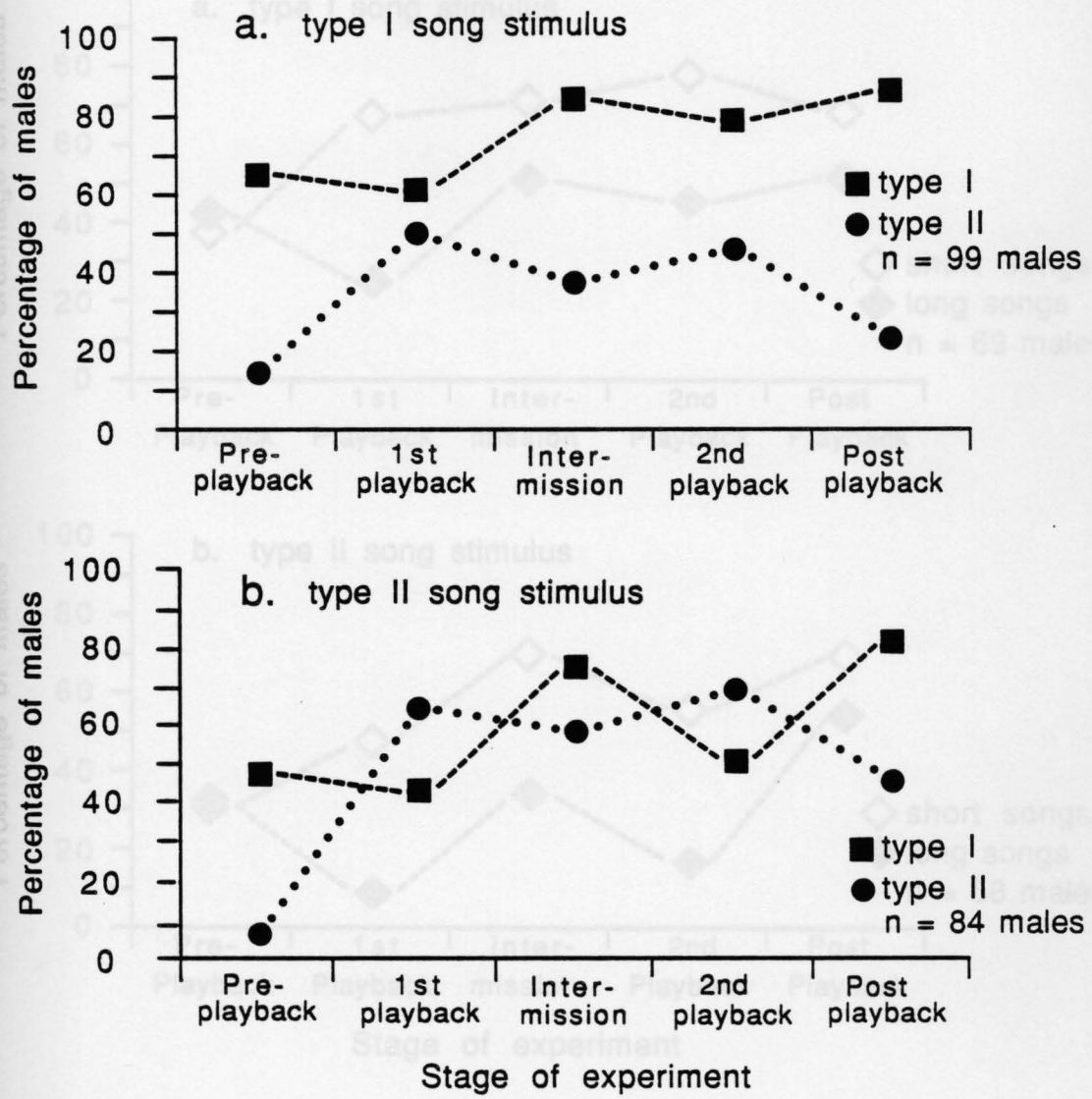


Figure 2.3. Changes in song type use by male Golden-winged Warblers during song playback experiments. Graphs show the percentage of males that sang type I and type II songs in each of five experimental periods. Change in type II use between the pre-playback and first playback periods was statistically significant ($P < 0.01$) for both categories of stimuli. Change in type I use between the same periods was not significant ($P >> 0.05$) for either type of stimulus. a. type I playback stimulus (median date 6 June, range 14 May - 29 June). b. type II playback stimulus (median date 19 June, range 24 May - 26 June).

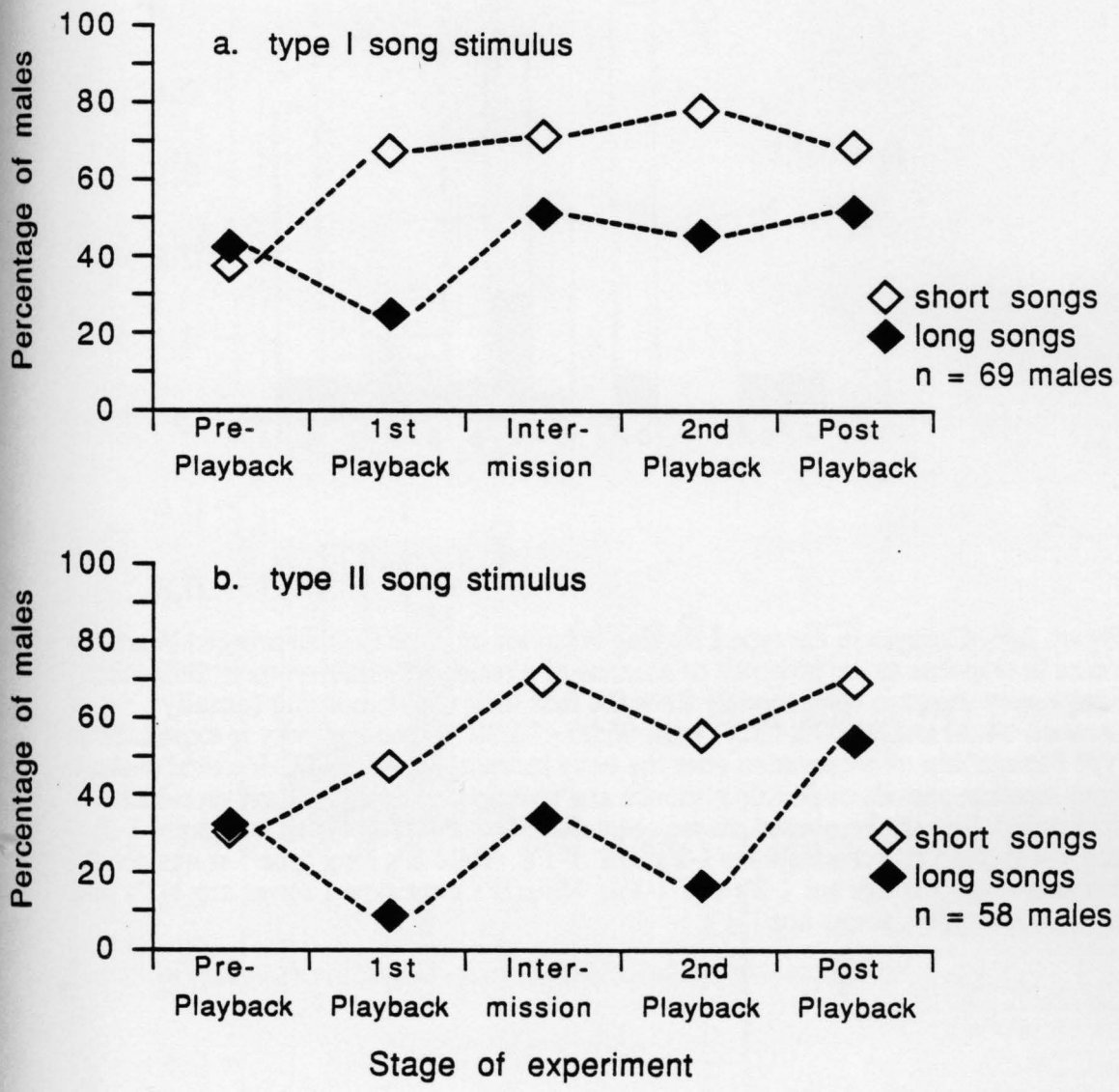
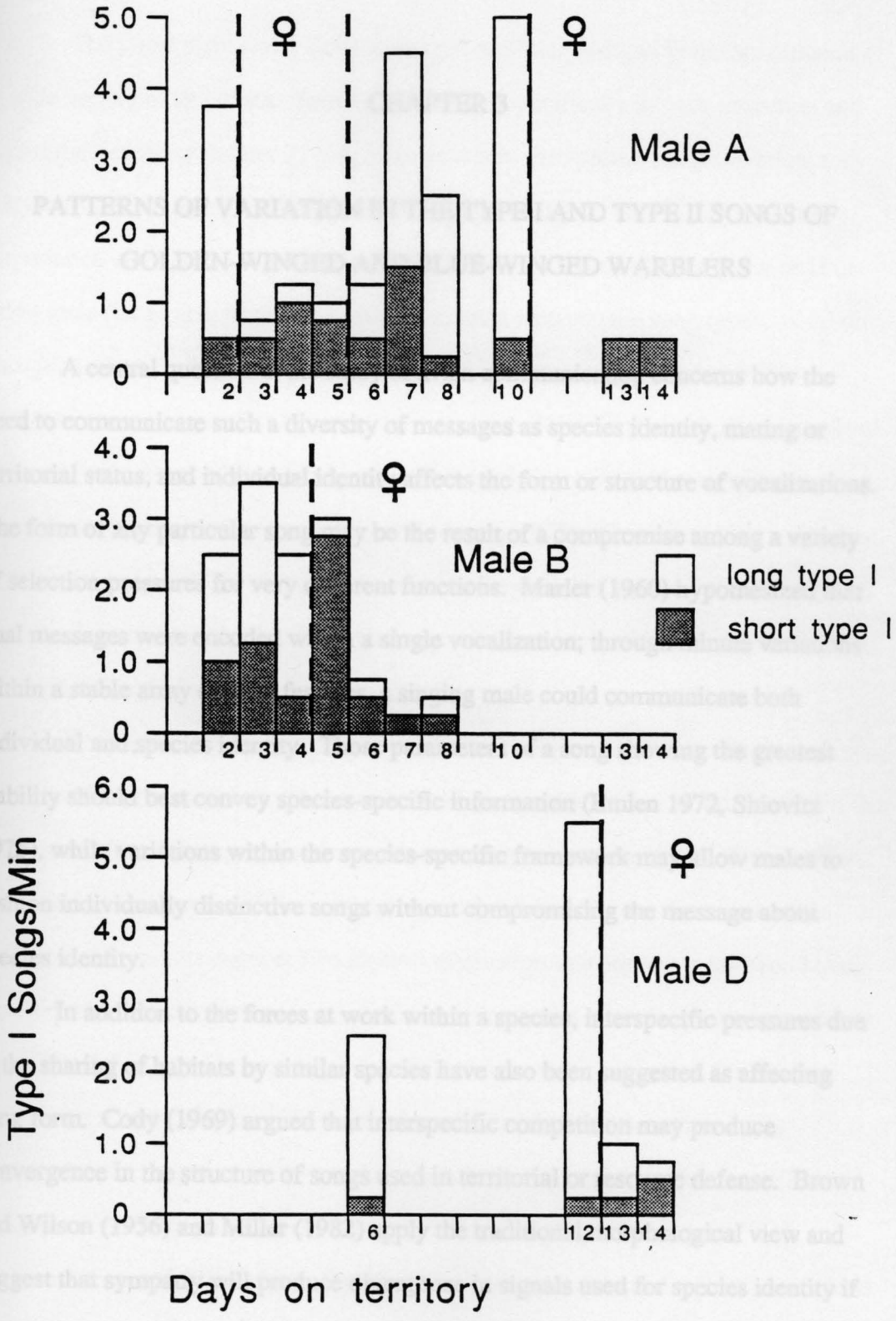


Figure 2.4. Changes in the length of type I songs sung by male Golden-winged Warblers during song playback experiments. Graphs show percentage of males who sang short (1-0, 1-1, 1-2) or long (1-3, 1-4, 1-5) type I songs in each of five experimental periods. Changes in the use of both short and long songs between the pre-playback and first playback periods were statistically significant ($P < 0.01$) for both categories of stimuli. a. type I playback stimulus. b. type II playback stimulus.

Figure 2.5. Changes in the type I singing behavior of three Golden-winged Warbler males in response to the presence or absence of a resident female on their territories. Songs were sampled continuously from the first song of the morning (usually between 04:50 and 05:00 h CDT) until 06:00 - 06:30 h. Song activity is expressed as type I songs/min of observation after the early morning type II bout. Vertical dashed lines separate periods of female presence and absence. Only those days on which data were taken are numbered on the abscissa. Male A's long type I songs are 1-3's and 1-4's; short type I songs are 1-2's and 1-1's. Male B's long type I songs are 1-3's; short type I songs are 1-2's and 1-1's. Male D's long type I songs are 1-2's and 1-3's; short type I songs are 1-1's.


Male A
Male B
Male D
long type I
short type I
Type I Songs/Min
Days on territory

CHAPTER 3

PATTERNS OF VARIATION IN THE TYPE I AND TYPE II SONGS OF GOLDEN-WINGED AND BLUE-WINGED WARBLERS

A central question in the study of avian communication concerns how the need to communicate such a diversity of messages as species identity, mating or territorial status, and individual identity affects the form or structure of vocalizations. The form of any particular song may be the result of a compromise among a variety of selection pressures for very different functions. Marler (1960) hypothesized that dual messages were encoded within a single vocalization; through minute variations within a stable array of song features, a singing male could communicate both individual and species identity. Those parameters of a song showing the greatest stability should best convey species-specific information (Emlen 1972, Shiovitz 1975), while variations within the species-specific framework may allow males to fashion individually distinctive songs without compromising the message about species identity.

In addition to the forces at work within a species, interspecific pressures due to the sharing of habitats by similar species have also been suggested as affecting song form. Cody (1969) argued that interspecific competition may produce convergence in the structure of songs used in territorial or resource defense. Brown and Wilson (1956) and Miller (1982) apply the traditional morphological view and suggest that sympatry will produce divergence in signals used for species identity if the inability to attract a conspecific mate and/or hybridization exact a cost in fitness.

The vocal displays of Golden-winged and Blue-winged Warblers function in a wide variety of situations. Songs are used intraspecifically in mate attraction and territorial defense (Chapter 2) and, in areas where the species' ranges overlap, may play a role in the interspecific interactions leading to hybridization. Even a brief experience with the type I and type II songs of an individual Golden-wing or Blue-wing male draws attention to the striking contrast between the song types. A minimal sampling of males from different geographic locations reveals another striking contrast; comparisons of song types from separate Blue-wing populations has shown that, while the form of type I songs appeared unchanged, type II songs varied considerably between locations (Gill and Murray 1972a, Kroodsma 1981). Further, Gill and Murray (1972a) claimed a correlation between the amount of song variation within a location and the degree of plumage introgression (evidence of hybridization) in the individuals found there.

Kroodsma (1981) suggested that different selection pressures on the two song types may be responsible for these patterns of geographic variation, but cautioned that such an explanation requires a clear understanding of song functions. The material I presented in Chapter 2 details a strong correlation between song form and song function. My results support Kroodsma's suggestion that stereotypy of type I song may be maintained by inter-sexual selection for a species specific vocal signal, while the "dialects" in type II song may be a result of intra-sexual selection for locally effective territorial displays. To determine whether these explanations apply throughout the ranges of the two species, it is important to verify that the differing patterns of variation in the two song types hold throughout the ranges of both Golden-wings and Blue-wings. By sampling from allopatric and mixed populations of both species, a further analysis of the effect of sympatry and/or hybridization on songs can be made.

A thorough description of Golden-wing and Blue-wing songs must be made before the songs can be compared geographically. Two previous studies focussed on such a description and their results may serve as a baseline for the present more extensive analysis. Lanyon and Gill (1964), working with an allopatric population of Blue-wings on Long Island, N. Y., provided the first systematic examination of songs in either species. They documented that each male's repertoire consisted of two distinct song patterns (type I and type II) formed from a small number of basic song components. Variation between males consisted mainly of "minor alterations in the duration and configuration of these components but did not include changes in their combination or sequence" (p. 17).

Gill and Murray (1972a) performed a more detailed analysis of songs in a Michigan population of birds that contained both species and hybrids. In addition to compiling a small set of frequency measures for the individual song components, they also compared the variability of overall song patterns with those found by Lanyon and Gill (1964) in New York. Their main conclusion was that songs of Blue-wings in Michigan, where they were sympatric with Golden-wings, showed fewer predominant overall patterns (i. e. less variability) than did the songs of the allopatric Blue-wings from Long Island. Although the difference was more pronounced in type I songs, the trend in type II songs was in the same direction. They also noted that the components of type II songs appeared to differ more between Michigan and New York than did the components of type I songs, suggesting differences between the song types in degree of geographic variability. Finally, they noted that hybridization in this mixed population seemed to produce a much greater number of birds that showed aberration in species typical plumage patterns than in song patterns, although they found a weak correlation between aberrance in song and in plumage.

The results of Gill and Murray (1972a) raise a number of interesting questions about patterns of song variation, the answers to which hinge on separating the effects of geography and the effects of sympatry and/or hybridization. Kroodsma (1981) replicated the result that type II varies more geographically with a comparison of two allopatric Blue-wing populations in New England. The question remains whether the differences in variability of the two song types are consistent across the species' range and if the same pattern obtains for Golden-wings. The questions concerning the effect of sympatry and interbreeding on songs require a baseline description of song parameters from a variety of locations with different histories of contact between the two species.

In the sections that follow I present the results of such an analysis. I describe songs from across the species' ranges both in terms of overall pattern of song components and in terms of a large number of frequency and temporal measurements of the components. I examine differences in variablility between mixed and allopatric locations and present the first systematic comparison of songs from birds of hybrid and of parental phenotypes.

Methods

I recorded Golden-winged and Blue-winged Warbler songs at 17 different geographic locations in May and June, 1984-1988 (Fig. 3.1, p. 80; see also Appendix). Except for the Itasca and Amherst sites, I spent one or two days at each location and attempted to record both song types from every territorial male I encountered. Most individuals were recorded in the morning or early afternoon (between 05:00 h and 13:00 h) but a small number were recorded in the early evening (between 18:00 h and 20:00 h). I frequently used cassette playback of type I and II

songs to attract males to within recording distance and to elicit type II songs. Only recordings that consisted of strong signals that were largely free of background noise were used for subsequent analysis. Additional recordings of Blue-winged Warblers from southeastern Minnesota and Ithaca, New York (made on my behalf by Bill Evans following the same protocol), and of Golden-wings from Tennessee (made by Don Kroodsma), and of hybrids (various locations, Library of Natural Sounds, Cornell Laboratory of Ornithology) were included in the analyses.

I used Scotch 209 or 809 recording tape and either a Uher 4200 Report Monitor or Uher 4200 Report Stereo IC tape recorder with a Dan Gibson EPM P-200 parabolic microphone for all recordings. The southeastern Minnesota and Ithaca Blue-winged Warbler recordings were made using a Marantz PMD 430 cassette recorder with a Sennheiser 816 microphone.

Songs were analyzed using SIGNAL sound analysis software (Engineering Design 1988) on an IBM AT computer. Songs were played into SIGNAL using a Tandberg Model 15-21 tape recorder and a Frequency Devices Model 901F anti-aliasing filter set at 10 kHz. Frequency and time measurements were made from sound spectrograms produced from a 512 point FFT (resolution = 49 Hz) or a 64 point FFT (resolution = 2.6 ms), respectively, using frequency and time cursors. Power spectra (16384 point transform) were done to determine the frequency of greatest amplitude of a song or song phrase. Amplitude modulation (AM) rate of song phrases was measured directly from the wave form by counting the number of pulses per unit of time (Fig. 3.2, p. 82). I determined the percent of amplitude modulation by measuring the distance from a peak to its base at three places within a phrase and using the average of these measures in the formula % AM = $100(E_{MAX} - E_{MIN}/E_{MAX} + E_{MIN})$, where E_{MAX} and E_{MIN} represent the upper and lower peaks, respectively, on an oscillogram (Mileaf 1967) (Fig. 3.2). Sound spectrograms used

in the examination of overall phrase and syllable morphology, and in the figures for this manuscript, were made on a Kay Elemetrics Co. Model 7029A Sonagraph (600 Hz filter).

Type I Song

Because preliminary examination of songs of the 12 hybrids I recorded showed that all sang a type I song easily recognizable as typical of one of the parental species, they were lumped together with the parentals (later analyses confirmed the similarities with parentals, see Results). I chose for measurement the two highest quality recordings from my sample of each male's type I singing, avoiding the use of consecutive songs when possible, and used the mean of the two songs measured per bird for all analyses except as noted below. A larger sample of type I songs from each of three color-banded males was used in order to assess variation in songs within individuals over different bouts or different days. Although I measured both A and B phrases of typical Blue-wing type I songs, I restricted my analysis to the A phrase and first B phrase of Golden-wing songs. Songs were subjected to the following measurements (Fig. 3.3, p. 84):

MaxA and MaxB = maximum frequency (Hz) of the A and B phrases, respectively.

MinA and MinB = minimum frequency (Hz) of the A and B phrases.

MfA and MfB = mean frequency (Hz) of the A and B phrases, eg. (MaxA + MinA)/2.

PeakA and PeakB = frequency (Hz) of greatest amplitude of the A and B phrases.

FrA and FrB = frequency range or bandwidth (Hz) of the A and B phrases, eg. (MaxA - MinA).

Fdiff = difference (Hz) between the mean frequencies of the A and B phrases, (MfA - MfB).

Pdiff = difference (Hz) between the frequencies of greatest amplitude of the A and B phrases, (PeakA - PeakB).

AmA and AmB = amplitude modulation rate (Hz) of the A and B phrases.

%AmA and %AmB = percent amplitude modulation of the A and B phrases, measured on only one song per male; %AmB not measured for Blue-wings.

DurA and DurB = duration (s) of the A and B phrases.

Interval = duration (s) of the interval between the A and B phrases.

Type II Song

Hybrids were lumped with parentals on the basis of whether they sang a Golden-wing or Blue-wing type I song. Because recordings of type II songs were often difficult to obtain and samples were usually much smaller than those for type I songs, only one type II song per male was used for analysis. I used sound spectrograms made on the Kay Sonagraph (300 Hz filter) to compile a catalog of the syllable types found in type II songs from all locations. In order to determine if song morphology correlated with geographic location, four "blind" judges sorted these spectrograms on the basis of overall similarity and syllable content. I used SIGNAL to make the following measurements of type II songs (Fig. 3.3):

- number of distinct syllables within a song.
- number of distinct syllable types within a song.
- peak frequency (Hz), i.e. frequency of greatest amplitude, measured over the entire song.
- duration (s) of the entire song.
- maximum frequency, minimum frequency, mean frequency, frequency of greatest amplitude, and frequency range or bandwidth (Hz), of the terminal or subterminal buzzy phrase (G syllable).

- amplitude modulation rate (Hz) of the terminal or subterminal buzzy phrase.

- duration (s) of the terminal or subterminal buzzy phrase.

Statistical Analysis

Statistical analysis of type I and type II measurements was done with the BMDP (Dixon 1985) and SPSS (Nie et al. 1975) statistical packages. The mean of the two songs measured per bird was used in the analysis for all comparisons involving type I songs except for variables %AmA and %AmB (measured only once per bird) and for the comparison of birds within locations (two songs per bird were used). I used ANOVA to determine population differences in type I and type II songs across geographic locations. I determined which locations were responsible for any significant effects through t-tests of all possible pairwise comparisons of locations. Significance levels for the pairwise t-tests across locations were determined using the Bonferroni multiple comparison procedure (Dixon 1985). T-tests were also used to make comparisons between different song groups (Golden-wings vs Blue-wings, Golden-wings vs hybrids, mixed populations vs non-mixed, etc.). Levene's test for equality of variances was used to determine whether probability values given for t-tests were based on pooled or separate variances.

Results

Type I songs

Syllable Morphology and Song Pattern. The Golden-wing and Blue-wing type I songs in my sample differed in overall song pattern and in syllable morphology. Golden-wing type I songs (Fig. 3.4, p. 86) typically consisted of 2 to 7 buzzy phrases with the initial phrase (A phrase) usually of higher frequency than those that followed (B phrases). Blue-wing type I songs consisted of a buzzy A

phrase followed by a single B phrase made up of discontinuous elements (Fig. 3.5, p. 88). The overall song pattern of Golden-wing type I songs may be described as "A-B_1-B_2-B_3..." and that of Blue-wings as "A-B."

A small number of males of both species used songs that differed from the more typical type I renditions. Some Golden-wings consistently sang a "monotone" type I song in which there was little or no frequency drop from the A to the B phrase (Fig. 3.6a, p. 90), and others showed a distinct down-slur at the beginning of the B phrases (Fig. 3.6b). One Itasca Golden-wing male (not recorded) sang several "A-B-A" patterned songs as well as normal songs in response to playback. Some Blue-wing males sang an A phrase that slurred gently upward or downward in frequency. Two Blue-wings sang songs with normal syllable morphology but with Golden-wing patterning (Fig. 3.6d) and another male had an irregularly patterned but otherwise normal B phrase (Fig. 3.6e). Two other Blue-wing males mixed "A-B-A" patterned songs in with the normal Blue-wing "A-B" songs (Fig. 36f).

Fine Structure of Type I Songs. For analysis of species differences in the fine structure of type I songs, I divided all birds, regardless of plumage phenotype, into one of two groups based on whether they sang a Golden-wing type I song or a Blue-wing type I song. Thus, 4 hybrids (all "Brewster's" phenotypes) and one phenotypic Blue-wing were lumped with 79 phenotypic Golden-wings in the Golden-wing song group (total = 84 birds from 14 locations). The Blue-wing song group consisted of 64 phenotypic Blue-wings and 7 hybrids (6 "Brewster's" and one "Lawrence's" phenotype) (total = 71 birds from 14 locations).

The Golden-wing song group and the Blue-wing song group were significantly different ($P < 0.01$) in every comparison of type I song measurements (Table 3.1, p. 59). In general, Golden-wing A phrases were higher in all frequency measures (MaxA, MinA, MfA, PeakA), but had a narrower bandwidth (FrA) than did

Blue-wing A phrases (Fig. 3.7, p. 94). For Golden-wings, on average, the peak frequency (PeakA) fell slightly below the mean frequency (MfA), but for Blue-wings this relationship was reversed.

Differences between the B phrases of the two species were much more complex and reflected their structural dissimilarity. Although the Golden-wing phrase was again higher in mean frequency (MfB), Blue-wing B phrases had a higher peak frequency (PeakB) (Table 3.1). The peak frequency of Golden-wing B phrases averaged very slightly higher than the mean frequency, but in Blue-wings the peak was greatly above the mean. The most striking difference in B phrase frequency measurements was the bandwidth; Blue-wing phrases had a very wide bandwidth (FrB) that bracketed the maximum and minimum frequencies (MaxB, MinB) of Golden-wing B phrases.

The frequency relationship between the A and B phrases gave each species' type I song a distinctive sound. Golden-wings showed a substantial drop in both mean frequency (Fdiff) and peak frequency (Pdiff) between the phrases (Table 3.1). Although mean frequency also dropped between phrases for Blue-wings, this difference was essentially cancelled out, on average, by an almost identical rise in peak frequency. The frequency drop in Golden-wings was easily discernible to my ear, but the pattern in Blue-wings was different from male to male. In some Blue-wings there seemed to be no frequency change between phrases but in others the B phrase sounded higher, presumably because the peak frequency was enough greater in amplitude that it stood out from the other frequencies present in the phrase.

The dramatic differences in amplitude modulation rate both between and within song groups were quite audible to the human ear; males with lower rates sounded much raspier than males with higher rates. Golden-wing A phrases had lower AM rates (AmA) than did those of Blue-wings, and they varied over a much

wider range of values (Table 3.1, Figs. 3.7 and 3.8, p. 96). Golden-wing B phrases resembled the A phrases in AM rate (AmB), but showed less variation. Blue-wing B phrases had the lowest AM rate of any of the four type I phrase types and varied over only a small range of values.

The percent of amplitude modulation (%AmA, %AmB) is a measure of how distinct a sound pulse was against the background amplitude of a song phrase. Although this measure is particularly sensitive to recording quality, and although I have no evidence that either humans or the birds themselves can hear the differences, the differences between groups are substantial (Table 3.1). The A phrases of Golden-wings showed higher percentages (i.e. they fell closer to zero amplitude between pulses of sound) than either Golden-wing B phrases or Blue-wing A phrases. The percent of modulation for the discontinuous Blue-wing B phrases was 100%.

There was extensive overlap in the duration of A phrases (DurA) of the two species, but Blue-wing B phrases were much longer than any of the other three phrase types. Because the number of phrases a Golden-wing male uses in his type I songs is highly variable (Chapter 2), B phrase duration of the two groups is not directly comparable. I thus made no attempt to compare the duration of entire songs between the two groups.

Fine Structure of Atypical Type I Songs. Song measurements revealed some of the differences between birds that sang typical songs and those that did not. Golden-wings that sang "monotone" songs had A phrases that were much lower than normal in all frequency measures. In some "monotone" males, the A phrase was so similar to the B phrase in both frequency and AM rate that it may be more accurate to consider these males as lacking an A phrase (Fig. 3.6a). For most of the Golden-wings that sang slurred B phrases, the higher frequency portion of the phrase was

essentially identical in frequency and AM rate to the A phrase (Fig.6b). The Blue-wings that had slurred A phrases or atypically patterned B phrases measured within the normal ranges for all variables.

Within Bird Variation in Golden-wing Type I Songs. To determine if I was justified in basing claims about group differences on samples of only two type I songs per male, I needed to assess whether a pair of songs recorded at a particular time was representative of the range of variation in song renditions. I accomplished this by recording three song samples from different days or different bouts for each of three color-banded Itasca Golden-wing males. I measured two songs from each sample and compared their mean values across days or bouts (Table 3.2, p. 60). There was little apparent variation in frequency variables or AM rate for songs from different samples of the same male (coefficients of variation usually fell between 0.02 and 0.05), but the duration of phrases was generally more plastic (coefficients of variation as high as 0.18).

Geographic Variation of Golden-wing Type I Songs. I tested for population differences in type I song measurements for birds that sang Golden-wing type I songs (Tables 3.3 - 3.6, pp. 61-64). I restricted my analysis to the 10 locations with samples from three or more birds (n = 80 birds: 77 Golden-wings, 3 "Brewster's") (Fig. 3.1, see also Appendix). Because including "monotone" songs created some problems with normality, the 7 birds that sang these songs were excluded from the analyses of all A phrase frequency and AM rate variables but were included in all other comparisons. "Monotones" were widely distributed geographically and their removal from the data set for this analysis was unlikely to alter the results (see below). Eliminating the "monotones" reduced the number of locations with three or more birds to 8 (n = 71: 70 Golden-wings, 1 "Brewster's") for those variables affected.

Seven of 19 variables (MaxA, FrA, PeakB, %AmB, Fdiff, Pdiff, and DurB) showed significant differences between locations ($P < 0.05$) (Tables 3.3 - 3.6, summary in Table 3.7, p. 65). T-tests of all possible pairwise comparisons of locations (28 separate comparisons for each frequency variable, 45 separate comparisons for all other variables) revealed that, in general, a significant location effect for a particular variable was attributable to differences between only a small number of locations. For example, in 3 out of the 7 variables that showed significant geographic variation (Fdiff, Pdiff, and DurB), the effect was due solely to differences between the two locations with the lowest and highest means (Table 3.5). For three other variables (MaxA, FrA, PeakB), location effects were attributable to single populations with very high or low means that differed significantly from several others (Tables 3.3, 3.4). Only variable %AmB, for which there were four significant pairwise comparisons, showed a more complex geographic pattern (Table 3.7).

The significant geographic differences in type I songs that ANOVA revealed were spread among a variety of variables and across most locations. Eight of the 10 locations were involved in at least one of the 16 total significant pairwise comparisons of these 7 variables. Even those locations that were involved in the greatest number of significant comparisons do not appear to differ from the other locations in any distinctive set of measures. The range of means for individual males from Mille Lacs, which has the lowest or highest population means for Fdiff, DurB, and %AmB, overlaps with those of all the other locations.

There was no clear geographic pattern in the occurrence of slurred B phrases or "monotone" songs among the total sample of 84 males and 14 locations. Seven of the 9 males that had slurred B phrases were from Minnesota (4 from Itasca, 3 from Mille Lacs), but the other two were from Caro, Michigan. I recorded 7 "monotone" males from 6 widely separated locations (one each from Itasca, Mille Lacs, Murphy-

Hanrehan, Caro, and Amherst; two from Vermont). I also encountered at least 3 additional "monotones" over the course of four seasons at Itasca, but was able to get only poor or no recordings.

Geographic Variation of Blue-wing Type I Songs. As in my comparison of Golden-wing type I songs, I restricted my analysis of Blue-wing type I songs to the locations from which I had samples of three or more birds (n = 65 birds from 9 locations: 58 Blue-wings, 6 "Brewster's", 1 "Lawrence's") (Fig. 3.1, see also Appendix). Nine of 18 variables (MaxA, MinA, MfA, MaxB, MinB, MfB, PeakB, Fdiff, Pdiff) showed significant differences between locations ($P < 0.05$, Tables 3.8 - 3.11, pp. 66-69, summary in Table 3.12).

The greater number of significant variables suggests more geographic variation for Blue-wings than for Golden-wings, but location differences for most single variables are still due to only a small number of locations (Table 3.12, p. 70). Although 8 of the 9 locations were involved in at least one of the 22 total significant pairwise t-tests (36 separate comparisons for each variable), comparisons involving Amherst or Columbia account for 15 of the 22. Differences between Amherst and Columbia alone accounted for the location effects for 5 of the 9 significant variables, including all of the significant differences in A phrase measures (MaxA, MinA, MfA). Although these two locations lie near the eastern and western extremes of the species' range, there does not appear to be any general longitudinal cline in A phrase frequency. In fact, the range of means for individual males from both Amherst and Columbia overlap extensively the ranges of all other locations for all 5 variables for which Amherst or Columbia has either the highest or lowest population mean.

The clearest evidence for widespread geographic variation is for the B phrase frequency measures (MaxA, MinB, MfB, PeakB); all but one of the recording locations are involved in significant pairwise comparisons for MfB (Table 3.12).

Still, 7 of the 9 significant comparisons are due to the effects of the two locations with the highest (Ithaca) or the lowest (E. Mass.) population means, and the range of MfB values for most locations except Ithaca and E. Mass. overlap extensively (Fig. 3.9, p. 98). Despite the appearance of significant variation between locations, predicting the location of origin for any particular song based on B phrase frequency would nonetheless be difficult.

My song sample of males that sang up- or down-slurred A phrases did show a clear geographic pattern; all 9 of these males were from Massachusetts (8 from Amherst, 1 from eastern Mass.). Consistent with this pattern were 3 males from Lanyon and Gill's Long Island population that also had down-slurred phrases (Lanyon and Gill 1964, their Fig. 5, p. 10) and the stated lack of such phrases in the Michigan populations studied by Gill and Murray (1972a, pp. 629-630).

Variations in overall song pattern did not appear to follow a clear geographic pattern. The two males that sang occasional "A-B-A" songs were from widely separated areas (Murphy-Hanrehan and Columbia). The two males that sang Blue-wing phrases with Golden-wing patterning were both from Amherst, but the male with the irregularly patterned B phrase was from Greer.

Variation of Type I Songs Within Locations. To properly assess the importance of geographic differences in song parameters, the variability between locations should be compared with the variability among males within a location. I tested for differences across birds within a location using the two largest geographic samples from each song group. At Itasca, differences across 26 individual Golden-wing males (n = 52 songs, df = 25, 26) were significant for all variables measured (one "monotone" male was excluded from the analysis so as not to bias results towards significance). All variables were significant at $P \leq 0.0001$ except for MaxA ($P = 0.0017$), DurB ($P = 0.0008$), and Interval ($P = 0.0002$). At Amherst,

differences across 21 individual Blue-wing males (n = 42 songs, df = 20, 21) were significant for all but two variables; MinB (P = 0.3252) and MfB (P = 0.0534). All other variables were significant at $P \leq 0.0001$ except for Interval (P = 0.0038) and FrB (P = 0.0181).

The results show not only that males within a location differed greatly from each other, but that the within location differences were generally more highly significant than the between location differences. A notable exception is the frequency of Blue-wing B phrases (MinB, MfB); the fact that Amherst males were very similar in these measures suggests that the significant location effects are meaningful.

Comparison of Hybrid and Parental Type I Songs. I compared the type I song measurements of all birds with Golden-wing plumage (n = 79) to birds of hybrid or Blue-wing plumage that sang a Golden-wing song (n = 5: 4 "Brewster's, 1 Blue-wing). Similarly, I compared the songs of all typical Blue-wings (n = 64) to the hybrids that sang Blue-wing songs (n = 7: 6 "Brewster's, 1 Lawrence's). Only one significant difference ($P < 0.05$) out of 37 separate t-tests was found in all comparisons between birds of parental and hybrid phenotypes; the drop in peak frequency from the A to the B phrase (Pdiff) was greater in Golden-wings than in the hybrid group (t = 2.42, df = 82, P = 0.0179). This difference is due to the fact that the Blue-wing and two of the "Brewster's" were "monotones" and had A phrases of lower than normal frequency. Except for these three individuals, the song measurements of all other Golden-wing or Blue-wing singing hybrids fell within normal species ranges.

In order to increase my sample of hybrid type I songs to compare with those of the parental species, I measured an additional 6 "Brewster's" and 1 "Lawrence's" (4 sang Golden-wing songs, 3 sang Blue-wing songs) that were recorded by other

workers (one bird from Halton recorded by R.D. James in 1983; 5 "Brewster's" from the Ithaca area and a "Lawrence's" from New Jersey by various recordists between 1960 and 1981, Cornell Library of Natural Sounds cut #'s 10746, 10747, 10749, 10752, 10827, and 27136). None of these birds were "monotones" and all of the 12 variables I measured (MaxA, MinA, MfA, FrA, MaxB, MinB, MfB, FrB, AmA, AmB, DurA, DurB) fell within the normal species ranges. Only one bird from Ithaca sang an unusual song; this male added a short section of what appeared to be a Blue-wing B phrase to the end of some renditions of his otherwise normal Golden-wing song (Fig. 3.6c).

There is thus little evidence to suggest that a mixed genetic makeup leads to the production of atypical type I songs. Of the total sample of 18 hybrids and 1 Golden-wing singing Blue-wing from 9 locations, 15 birds from 7 locations sang typical Golden-wing or Blue-wing type I songs.

Comparison of Type I Songs From Mixed and Non-mixed Locations. As suggested by the results of Gill and Murray (1972a, b), I looked for an effect of sympatry of the two species on the form of type I songs. I had song samples from only three locations (Hope, Caro, and Vermont; see descriptions in Appendix) that I considered to be truly mixed at the time I made the recordings, i.e. areas in which singers of Golden-wing and Blue-wing type I songs were almost equally numerous and were intermingled spatially. I decided not to consider areas like Amherst as mixed where, although 8 widely separated Golden-wing or hybrid territories were found over two seasons, the probability that a particular Blue-wing male would have any contact with a Golden-wing type I song was quite low (only 3 of the 8 birds sang a Golden-wing song). Although any of the other areas where I found hybrids present (Chelsea, Audley, Ithaca, Amherst) were presumed to have had a more mixed

population in the past, I believe it is best to use for comparison only those populations whose current status I know.

I looked for consistent differences between mixed and non-mixed populations in several ways. First, I compared overall means of the song variables for each Golden-wing ("monotones" were included) or Blue-wing song group by combining the three mixed locations into a single large mixed group and comparing them to the combined non-mixed locations. Because this lumping of locations may have obscured differences due to single locations, I also compared birds from each mixed group with those of the single nearest non-mixed population. Lastly, because groups may differ greatly in variablility even if they share similar means, I compared the variances of the mixed and non-mixed groups. If sympatry has had a consistent effect on the form of type I songs, I would expect to find consistent patterns in which variables are involved and/or in the direction of differences between groups (e.g. that mixed groups were consistently more or less variable than non-mixed).

The comparisons of the mixed and non-mixed groups for birds that sang Golden-wing songs revealed only a small number of significant differences between group means (Table 3.13, p. 71). Despite the large number of individual tests (76 total, 19 variables in each of 4 separate comparisons), none of the differences were significant below $P = 0.01$. There were more significant differences among the variance comparisons, 6 of which were significant at $P < 0.01$ (Table 3.14, p. 72). Out of the 15 significant comparisons ($P < 0.05$), the mixed group was more variable than the non-mixed group in 10 instances. The only clear pattern was for comparisons of mixed locations containing "monotones" (Caro had one "monotone"; in Vermont, 2 of the 3 birds were "monotones") and a nearest non-mixed location with no "monotones" (Pellston and Gravenhurst).

Comparisons between the mixed and non-mixed groups that sang Blue-wing songs also revealed only a small number of significant differences in population means ($0.05 > P > 0.01$ for all 4, Table 3.15, p. 73). Because Chelsea, the nearest currently non-mixed Blue-wing population to Hope and Caro, had Golden-wings within the recent past, I also tested the mixed group against Columbia, where the incidence of Golden-wings is very rare. There were a total of 6 significant differences in variances between mixed and non-mixed groups (the mixed group was the more variable in two instances), but no pattern was obvious (Table 3.16, p. 74).

There was also no obvious pattern between mixed and non-mixed locations in the occurrence of atypical songs. Although the most striking differences in variance between Golden-wing song groups were due to the presence of "monotones", only 3 of the 7 "monotones" present in my sample were from mixed locations. Slurred Golden-wing B phrases were present in both mixed (Caro) and non-mixed (Itasca, Mille Lacs) locations. None of the aberrant song patterns occasionally found in Blue-wing songs were found in any of the mixed locations.

Type II Songs

Syllable Content and Order of Type II Songs. In contrast to the relatively stereotyped phrases of the type I songs, a variety of syllable types characterized the type II songs of Golden-wings and Blue-wings (Fig. 3.10, p. 100). Males of both species typically sang songs with 6 to 13 syllables of 2 to 4 different syllable types, usually ending with a terminal or subterminal buzzy phrase superficially similar to a type I B phrase. Although the order of syllable types within a song was invariant, individual males often varied how many syllables of a particular type they used from rendition to rendition. Less commonly, males omitted the last 1 to 3 syllable types from some renditions of their type II songs (Chapter 2). For example, the male in Fig. 3.10a sang 1 to 3 A syllables, from 4 to 8 B syllables, from 1 to 2 F syllables,

and sometimes omitted the terminal buzz (G syllable) in different song renditions, but syllables were always sung in the order A-B-F-G.

Because differences between type II songs of the two species were not as immediately obvious as were the differences between type I songs, I analyzed songs on the basis of syllable content. I divided type II syllables from the entire geographic song sample into eight broad groups defined by syllable morphology and order of occurrence within songs (Fig. 3.11, p. 104). Group A syllables were repeated 1 or 2 times, often very softly, and were always used as introductory notes. Group B, C, and D syllables were usually repeated 2 to 8 times and always followed group A syllables. Syllables from these groups were usually the most numerous syllable type within a song. Syllables from group E were almost identical in use to those from groups B, C, and D, with the exception that some Massachusetts Blue-wings appended 1 or 2 of them at the very end of a song. Group F syllables were typically sung only once or twice and always fell between group B syllables and the terminal buzz (group G). Group G syllables comprise buzzy phrases of essentially constant frequency, although sometimes with brief initial up- or down-sweeps in frequency, that were usually placed at the end of a song. Group H syllables, buzzy phrases that swept downward in frequency, also occurred commonly at the end of a song.

Species Differences in Type II Songs. Out of the 13 total subgroups that I recognized (Fig. 3.11), a relatively small number of syllable types were restricted to a single species. Syllable types A2, B, F1, F2, and G2 were found only in Golden-wings and only a single syllable, type E2, was restricted to Blue-wings.

Song measurements revealed additional differences. Although there were no significant differences in the number of syllables per song or in the peak frequency measured across whole songs, Golden-wing type II songs averaged slightly longer and had more syllable types per song than did Blue-wings (Table 3.17, p. 75). The

species also differed significantly in 6 out of 7 measurements of the group G buzzes, the syllable type with the widest geographic range (Table 3.17). Golden-wing G syllables tended to be longer, of lower frequency, and narrower in bandwidth than those of Blue-wings.

Geographic Variation in Type II Songs. I assayed the geographical distinctiveness of type II songs through the use of four "blind" judges who sorted songs on the basis of overall similarity and syllable content. To analyze their results, I looked at the percentage of songs from each location that judges assigned to the same group, and into how many groups songs from each location were split if not all were placed in the same group. I also determined the total number of song groups each judge made from the entire sample of songs and how many of those groups were geographically pure, i. e. consisted of songs from a single location. In general, both accuracy in grouping together songs from the same location and agreement between judges was high (Table 3.18, p. 76).

Although few of the actual geographic groupings were recreated by any judge, over half of the judge's total song groups were geographically pure (Table 3.18). When performance was averaged over judges, songs from the same location were grouped together with 100% accuracy for 4 of the 13 locations and with greater than 80% accuracy for 10 locations. Accuracy for individual judges was much higher. Even songs from the two locations with the largest samples, Itasca and Amherst, were each split into only 2 or, on one occasion, 4 groups. Judges had most difficulty with songs from Hope (8 songs split among 3 to 4 groups) and Caro (6 songs split among 2 to 3 groups), the two sympatric locations in Michigan where the species are spatially intermixed.

Despite the judges' ability to sort whole songs by location, most syllable types were not confined to particular geographic areas (Table 3.19, p. 77). The

terminal or subterminal buzz (G syllable) was the single most geographically common element, variants of which occurred in 15 out of the 17 locations. Although some birds had both a G and an H syllable, every bird that lacked a G syllable (6 birds from 4 locations) had instead an H syllable. The A1 variant of the introductory syllables was the second most widespread, present at 12 locations. Syllable types that were wholly or nearly restricted to one species were also found in widely separated locations; group B syllables, used only by Golden-wings, were found from Itasca to Amherst and group D syllables, found primarily among Massachusetts Blue-wings, appeared as far west as Hope, Michigan. Only group F syllables were restricted in this sample to one species at one location (Golden-wings at Itasca), but a Blue-wing recorded by Eugene Morton in Pennsylvania also used this very distinctive syllable in his type II song.

Analysis of variance of whole song variables showed that Golden-wings differed geographically only in the number of syllable types per song but that Blue-wings and both species combined varied significantly in almost all measures. Analysis of variance of G syllables across locations showed patterns of variation in frequency and temporal measures similar to those for the type I phrases.

Comparison of Hybrid and Parental Type II Songs. Songs of hybrids did not appear noticeably different from the other type II songs present at their locations. At Amherst, 2 Brewster's and 1 Lawrence's that sang normal Blue-wing type I songs also sang type II songs typical of Blue-wings at that location. At Ithaca, two Brewster's that sang Blue-wing type I songs had type II songs that closely resembled a neighboring Blue-wing, and the type II songs of a Golden-wing and a Brewster's with a Golden-wing type I song at Vermont were very similar.

Comparison of Type II Songs From Mixed and Non-mixed Locations. Species differences in syllable content or song measures of type II songs are not

readily apparent when comparisons are made within locations. At Amherst, although one Golden-wing sang a song that all judges agreed was unique in the entire geographic sample, the two other Golden-wings present sang songs indistinguishable from the 18 local Blue-wings. At Hope, the songs of two Blue-wings each resembled the songs of one or more Golden-wings more than they resembled each other (Fig. 3.12, p. 106). The single Golden-wing at Columbia sang a typical local Blue-wing type II, but the only Blue-wing sample from Caro had D and G3 syllables not seen in the 5 Golden-wing type II songs. Unlike the data for type I songs, whole song and G syllable variables for the minority species at each location overlap in almost all measures with those of the more common species.

Two of the mixed locations, Hope and Caro, appeared to show a greater variety of type II song forms than any of the other areas. Despite the smaller sample of songs from these locations, the judges split them into more groups (mean number of groups: Hope = 3.5, Caro = 2.75) based on overall similarity and syllable content than they did the much larger samples from Itasca (mean = 2.5) and Amherst (mean = 2.0). The total number of syllable variants present in songs from Hope (8) and Caro (7) exceeded or equaled those from the Itasca (7) and Amherst (5) samples (Table 3.18). The sample of type II songs from Columbia, identical in size to that of Hope, was lumped into a single group by all judges (Table 3.17) and contained a total of only 3 syllable types.

Discussion

Analysis of recordings made at over 20 widely separated locations confirms the notion that the two song types show very different patterns of variation between the two species, between geographic locations, and within populations. A male's

type I song was generally an excellent predictor of his species (based on plumage pattern), but type II songs revealed more about an individual's geographic status than his specific status.

Type I Songs Showed Distinct and Consistent Species Differences

Even when males that sang atypical songs were included in the analysis, the type I songs of Golden-wings and Blue-wings were distinct in every measure of frequency and rate of amplitude modulation (Table 3.1). Despite the similarity in overall form of three of the four phrase types (Golden-wing A and B phrases, Blue-wing A phrase), they were easily separable on the basis of mean frequency and AM rate alone (Fig 3.7). Of the males of either species that showed aberration in overall song pattern (Fig. 3.6, p. 90), only Golden-wings that sang "monotone" songs differed consistently from the norm in any set of measures.

Type I Songs Were Highly Stereotyped Geographically (Figs. 3.4 and 3.5)

Attempting to sort type I songs into geographic groups based on song measurements, or on a visual examination of sonograms (as was done successfully for type II songs), would prove extremely difficult for two reasons. First, even though the population means of nearly half the type I song variables differed significantly across recording locations, the degree of song variation within locations may tend to swamp variation between locations. At the two locations with the largest sample for each species (Itasca and Amherst), differences between males within a location were more highly significant than were the location effects for the same variables in all but two cases. Secondly, even for the variable that provided the most suggestive evidence for geographic distinctiveness (the mean frequency of Blue-wing B phrases), the range of values for individual males overlapped extensively across locations (Fig. 3.9).

The only features that impart a geographic distinctiveness to type I songs are certain uncommon gross characteristics, such as the slurred B phrases of some Minnesota and Michigan Golden-wings (Fig. 3.6) and the up- or down-slurred A phrases of some New England Blue-wings. The degree of slurring in the songs of different males of both species ranged from pronounced to barely noticeable on a sonogram, and only extreme examples were audible to the practised human ear. Despite the unusual qualities of these songs, birds may well perceive them as falling within an acceptable continuum of variation in phrase "shape", similar to the wide range of variation found within populations for other song characteristics (e.g. amplitude modulation rate and the drop in frequency between A and B phrases for Golden-wings, mean frequency of the B phrase for Blue-wings). This sort of variation within an overall stable array of song parameters is reminiscent of Marler's (1960) notion concerning the kind of traits potentially useful in individual recognition (see also Gill and Murray 1972a). Playback experiments with naive males from other locations would be required to determine whether or not slurred songs elicited normal responses.

Widespread Geographic Variation Obscured Species Differences in Type II Songs

Description of species differences in type II songs was confounded by the large degree of geographic variation these songs showed. Song measurements produced a number of highly significant differences between Golden-wing and Blue-wing songs (Table 3.17), but there was a general lack of species-specificity of the component syllable types (Table 3.19). Even though few syllable types were geographically confined, "blind" judges were able to group together type II songs from the same location with a high degree of accuracy (Table 3.17). Songs were reliably identified to species only if they exhibited syllable combinations that were unique to a location, such as Itasca or Columbia, that was populated almost

exclusively by a single species. Unfortunately, sample sizes of type II songs from sympatric populations were too small to allow the kind of analysis that could separate species characters from location differences.

The form of type II songs did not correlate with species typical plumage patterns in populations where both species occurred. I found examples in Amherst, Hope, and Columbia of males with Golden-wing plumage that sang songs very similar to those of males with Blue-wing plumage at the same location. This runs counter to the observations of Gill and Murray (1972a), who reported that neither species sang the type II song of the other in the mixed populations they studied in Michigan.

Song Form is Correlated With Song Development and Song Function

The different patterns of geographic variation that I described for the two song types support the ideas of Kroodsma (1988) that the ontogeny of type I songs is less dependant on social interaction and imitation than is the ontogeny of type II songs. Kroodsma raised Blue-wing nestlings in the laboratory and tutored them with tape recordings of conspecific songs. Although none of the birds produced normal wild-type songs, their type I songs showed a much higher degree of resemblance to the tutor songs than did their type II songs. For example, all of the 14 experimental males produced a recognizable Blue-wing A phrase (as did a single female that had been implanted with testosterone), but none of them sang a good copy of the type II songs. The observed stereotypy of type I songs across locations may be a direct manifestation, on a proximate level, of a genetically constrained development of type I song components. In contrast, the impressive geographic variety in type II songs may have resulted from ontogenetic processes that are dependant upon social interactions and song copying between males.

The form and development of songs in these species are also correlated with the functions they serve. The songs (type I) that males use in mate attraction (Chapter 2), a function for which species specificity is of great importance, are also the least variable and most developmentally constrained of the songs in their repertoires. On the other hand, the songs (type II) that are used almost exclusively in male-male interactions (Chapter 2) are highly variable in form and may be more subject to local cultural influences, rather than to genetic influences, during development.

Songs of Hybrids Did Not Generally Differ From the Songs of the Parental Species

In light of the data on song development in these species, it might be expected that hybridization would produce males that sang normal type II songs (learned through social interactions) but whose type I songs blended species typical characteristics. Nevertheless, I found that hybrids did not consistently differ from the parental species in the form of either song type. Although 3 out of 5 hybrids that sang Golden-wing type I songs were "monotones," songs with atypical features were by no means restricted to, or even most common in, hybrids. This analysis was complicated by the fact that birds of apparently normal plumage may nonetheless have a mixed genetic make-up, but it is clear that no strong correlation between the degree of introgression in plumage and in song was found. Although hybridization results in intermediate plumage patterns, it does not appear to result in intermediate singing behaviors.

Do Interspecific Interactions Affect the Form of Type I Songs?

According to the traditional view (e.g. Brown and Wilson 1956, Mayr 1963), the form of signals that function in communication between mates should diverge between species in areas where interspecific hybridization results in offspring with reduced fitness. Although hybrids between Golden-wings and Blue-wings are viable and capable of reproduction, they have nonetheless been observed to acquire mates

less frequently, and later in the season, than males of the parental species (Ficken and Ficken 1968a). Theory would thus predict that the mate attraction songs (type I) of these species should not only be distinctive but might well show exaggerated differences in sympatry.

I found no clear evidence that type I songs of the two species were more distinctive in sympatric than in allopatric populations. These results are contrary to those of Gill and Murray (1972a), who found that type I songs of Blue-wings from a sympatric population in Michigan showed less variation (i.e. fewer predominant song patterns), and thus greater distinctiveness, than did the songs of an allopatric population in New York. Song patterns other than the species typical A-B (Blue-wings) or A-B_1-B_2-B_3 (Golden-wings) were extremely rare in all the populations that I examined. I also assessed variation in the structural characteristics of the individual phrase types but again found no differences. Type I songs appeared neither more nor less similar in the mean of song measures in mixed populations, nor did they seem more or less variable than non-mixed populations in any consistent set of parameters (Tables 3.13 - 3.16.)

There are several possible, non-mutually exclusive, explanations for the lack of effects of interspecific interactions on the two species' songs. First, the cost in reproductive fitness of mistaken species identity and/or hybridization may not be high enough to drive selection for type I song divergence. Hybrids are quite viable and their tendency to backcross with parental forms rather than to form hybrid-hybrid pairs may slow any dilution of locally adapted genotypes (Ficken and Ficken 1968c, Gill and Murray 1972b). Further, because only a low level of genetic divergence is evident even between phenotypically "pure" individuals of both species (as revealed by allozyme analysis, Gill 1987), significant blending of genotypes due to hybridization might not have detrimental effects.

Second, even if substantial fitness costs are associated with sympatry, the unusually rapid expansion of Blue-wings into Golden-wing range (Gill 1980) may outpace any effects of selection. Although they now comprise about 50% of the *Vermivora* population at the Hope, Michigan site, Blue-wings were unknown there as a breeding species less than 25 years ago (Will 1986). Third, despite its apparent value as a species-specific character, type I song may function only weakly in species discrimination relative to other traits such as plumage (but see Chapter 4). Fourth, the sample sizes in my comparisons between mixed and non-mixed locations may have been insufficient to detect the differences in variability I was seeking.

A fifth possibility is that the differences in type I songs between Golden-wings and Blue-wings did not result from interspecific selection for species recognition, and therefore no effect of sympatry would be expected. Payne (1983) and West-Eberhard (1983) have suggested that it is mainly the combined effects of selective forces acting within a species, rather than between species, that are responsible for the variety of song forms we see in nature. Mate choice by females (intersexual selection) and competition among males for limited resources (intrasexual selection) may act together to produce patterns of variation in signals very similar to patterns expected from selection for reproductive isolation. A shortcoming of this argument for the case at hand was foreseen by Payne, who noted that "if bird songs had been selected mainly at the level of species distinctiveness, then one would expect a developmental pathway that was more dependant on species-specific genetic determinants..." (1983, pp. 56-57). Kroodsma's (1988) experiments in song ontogeny suggest that, for the Blue-wing A phrase at least, the development of type I songs may be highly genetically determined.

Do Interspecific Interactions Affect the Form of Type II Songs?

Cody (1969) and Brown (1977) have stated that convergence of signals used by males to communicate aggression may be expected in areas of sympatry if the species involved exhibit interspecific territoriality. Both Murray and Gill (1976) and Will (1986) report that, although Golden-wing and Blue-wing males do interact agonistically, territories overlap extensively (59% on average at Hope, Michigan; Will 1986) and are defended only intra-specifically. There thus appears to be little reason to expect a marked effect of sympatry on the form of type II songs.

Nevertheless, and unlike the results for type I songs, sympatry did correlate with a greater variety of type II song forms. The sample populations in which Golden-wings and Blue-wings intermingled to the greatest extent (Hope and Caro, Michigan) also proved to be the sites of the greatest diversity in type II songs (Fig 12). Both of these locations are near the northern limit of Blue-wing range in this area and thus lie in the path of the generally northward expansion of that species (Gill 1980, Will 1986). Perhaps the most likely scenario is that Blue-wings immigrating to these areas enriched the existing variety of song forms with new syllables and syllable combinations from their populations of origin. This same phenomenon could occur wherever formerly separated populations, whether of the same or of different species, came into contact. In the present case, only the species typical plumage differences signaled to me that these populations consisted of birds of historically different geographic origins.

Future Directions for Study of Song Variation in Golden-winged and Blue-winged Warblers

A long term study that followed a currently allopatric Golden-wing population(such as Itasca) through the stages of early and later sympatry with Blue-wings could untangle many of the questions concerning the effect of species

interactions on song form. One would need a thorough catalog of existing type I and II songs from a large surrounding area in order to document local changes and to be able to assign the origin of new song variants to either the other species or to another geographic locality.

Table 3.1. Differences between type I song groups. Shown are mean ± SD (coefficient of variation) of type I song variables for birds that sang Golden-wing songs (n = 84) and birds that sang Blue-wing songs (n = 71). Groups differed significantly for all variables (t-test, $p < 0.007$). Variables in this and in subsequent tables are described in the text.

	Golden-wing	Blue-wing	
MaxA (Hz)	9008 ± 449 (0.05)	7645 ± 361 (0.05)	
MinA (Hz)	6646 ± 592 (0.09)	5112 ± 553 (0.11)	A phrase
MfA (Hz)	7827 ± 487 (0.06)	6379 ± 429 (0.07)	frequency
PeakA (Hz)	7524 ± 479 (0.06)	6473 ± 615 (0.10)	variables
FrA (Hz)	2362 ± 393 (0.17)	2533 ± 367 (0.14)	
MaxB (Hz)	7792 ± 336 (0.04)	8041 ± 358 (0.04)	
MinB (Hz)	5119 ± 438 (0.09)	3703 ± 324 (0.09)	B phrase
MfB (Hz)	6455 ± 332 (0.05)	5872 ± 271 (0.05)	frequency
PeakB (Hz)	6595 ± 471 (0.07)	6922 ± 597 (0.09)	variables
FrB (Hz)	2673 ± 413 (0.15)	4284 ± 657 (0.15)	
Fdiff (Hz)	1371 ± 517 (0.38)	506 ± 553 (1.09)	frequency difference
Pdiff (Hz)	928 ± 603 (0.65)	-449 ± 1001 (2.23)	between phrases
AmA (Hz)	132 ± 37 (0.28)	235 ± 13 (0.06)	
AmB (Hz)	146 ± 18 (0.12)	40 ± 2 (0.05)	amplitude modulation
%AmA (%)	59 ± 13 (0.22)	39 ± 10 (0.26)	variables
%AmB (%)	44 ± 12 (0.27)	--- ± --- (----)	
DurA (s)	0.450 ± 0.09 (0.20)	0.583 ± 0.09 (0.16)	temporal
DurB (s)	0.301 ± 0.05 (0.16)	0.715 ± 0.17 (0.19)	variables
Interval (s)	0.05 ± 0.0 (0.19)	0.04 ± 0.01 (0.26)	

Table 3.2. Variation in type I songs from three Itasca Golden-winged Warbler males (3 samples of song bouts per male). Values shown are the means of the two songs measured per sample, and the overall mean and coefficient of variation based on the three sample means.

Bird # 1	30 May	5 June	11 June	Overall	C. V.
MfA (Hz)	8003	8003	7991	7999 ± 6.9	(0.0009)
PeakA (Hz)	7474	7434	7434	7447 ± 23	(0.003)
MfB (Hz)	6540	6159	6171	6290 ± 216	(0.03)
PeakB (Hz)	6073	6133	6530	6245 ± 248	(0.04)
AmA (Hz)	90	88	87	88 ± 1.5	(0.02)
AmB (Hz)	155	151	150	152 ± 2.6	(0.02)
DurA (s)	0.580	0.560	0.560	0.566 ± 0.1	(0.17)
DurB (s)	0.410	0.370	0.350	0.376 ± 0.03	(0.08)

Bird # 2	30 May	5 June	12 June	Overall	C. V.
MfA (Hz)	7732	7794	7880	7802 ± 74	(0.009)
PeakA (Hz)	7415	7465	7693	7524 ± 148	(0.02)
MfB (Hz)	6565	6576	6564	6568 ± 6.6	(0.001)
PeakB (Hz)	6888	6500	6033	6473 ± 428	(0.07)
AmA (Hz)	136	134	138	136 ± 2.0	(0.01)
AmB (Hz)	140	134	140	138 ± 3.4	(0.03)
DurA (s)	0.310	0.340	0.340	0.330 ± 0.02	(0.06)
DurB (s)	0.230	0.220	0.210	0.220 ± 0.01	(0.05)

Bird # 3	31 May	5 June (am)	5 June (pm)	Overall	C. V.
MfA (Hz)	7822	7352	7659	7611 ± 238	(0.03)
PeakA (Hz)	7325	7236	7335	7298 ± 54	(0.007)
MfB (Hz)	6208	6281	6417	6302 ± 106	(0.02)
PeakB (Hz)	5854	6302	5914	6023 ± 243	(0.04)
AmA (Hz)	147	136	150	144 ± 7.3	(0.05)
AmB (Hz)	147	145	142	145 ± 2.5	(0.02)
DurA (s)	0.240	0.340	0.280	.0286 ± 0.05	(0.18)
DurB (s)	0.200	0.220	0.220	0.213 ± 0.01	(0.05)

Table 3.3. Population means ± SD of frequency (Hz) variables for A phrases from Golden-winged Warbler type I songs. Nine males that sang "monotone" songs are excluded from the analysis. Significance levels are given for differences across locations as determined by ANOVA (n = 71 birds, df = 7, 63) and are not adjusted for the number of separate tests (in this and all subsequent tables * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$).

Location	MaxA	MinA	MfA	PeakA	FrA
Tenn. (N=3)	9590 ± 107	6508 ± 418	8048 ± 219	7856 ± 298	3082 ± 422
Itasca (N=27)	9140 ± 241	6733 ± 486	7937 ± 294	7566 ± 339	2406 ± 403
Mille Lacs (N=9)	8997 ± 251	6746 ± 486	7871 ± 298	7630 ± 200	2250 ± 494
Pellston (N=8)	9036 ± 215	6682 ± 230	7859 ± 206	7453 ± 275	2354 ± 169
Hope (N=7)	8933 ± 246	6846 ± 280	7889 ± 190	7574 ± 291	2087 ± 366
Caro (N=7)	8991 ± 312	6729 ± 323	7860 ± 285	7492 ± 297	2262 ± 278
Halton (N=5)	9319 ± 286	7076 ± 414	8197 ± 344	7968 ± 606	2243 ± 183
Grvhurst (N=8)	9131 ± 330	6909 ± 185	8020 ± 238	7724 ± 238	2222 ± 242
Overall (N=8)	9142 ± 217	6778 ± 168	7960 ± 120	7658 ± 179	2363 ± 305
C. V.	(0.02)	(0.02)	(0.01)	(0.02)	(0.13)
P	0.0092**	0.4674	0.3820	0.1237	0.0144*

Table 3.4. Population means ± SD of frequency (Hz) variables for B phrases from Golden-winged Warbler type I songs. Significance levels are given for differences across locations as determined by ANOVA (n = 80 birds, df = 9, 70) and are not adjusted for the number of separate tests.

	MaxB	MinB	MfB	PeakB	FrB
Tenn (N=3)	7983 ± 284	5130 ± 61	6556 ± 113	6649 ± 231	2853 ± 343
Itasca (N=27)	7705 ± 365	5128 ± 437	6416 ± 358	6261 ± 505	2577 ± 368
Mille Lacs (N=9)	8130 ± 423	5447 ± 774	6789 ± 533	6817 ± 420	2683 ± 648
Pellston (N=8)	7659 ± 255	5056 ± 454	6357 ± 332	6816 ± 194	2603 ± 320
Hope (N=7)	7742 ± 112	5272 ± 407	6507 ± 227	6911 ± 186	2469 ± 387
Caro (N=7)	7675 ± 302	4917 ± 223	6296 ± 204	6426 ± 573	2758 ± 342
Halton (N=5)	7873 ± 288	5055 ± 76	6464 ± 144	6840 ± 265	2818 ± 308
Grvhurst (N=8)	7807 ± 282	5145 ± 290	6476 ± 201	6842 ± 343	2662 ± 408
Vermont (N=3)	7794 ± 195	5122 ± 465	6458 ± 208	6454 ± 434	2672 ± 580
Amherst (N=3)	7918 ± 277	4729 ± 233	6323 ± 174	6905 ± 100	3189 ± 375
Overall (N=10)	7828 ± 149	5100 ± 191	6464 ± 141	6692 ± 232	2728 ± 198
C. V.	(0.02)	(0.04)	(0.02)	(0.03)	(0.07)
P	0.0838	0.3802	0.1832	0.0006***	0.4113

Table 3.5. Population means ± SD of frequency (Hz) and temporal (s) variables from Golden-winged Warbler type I songs. Nine males that sang "monotone" songs were excluded from the analysis for Fdiff and Pdiff (n = 71 birds, df = 7, 63) but not from the analysis of DurA, DurB, or Interval (n = 80 birds, df = 9, 70). Significance levels are given for differences across locations as determined by ANOVA and are not adjusted for the number of separate tests.

	Fdiff	Pdiff	DurA	DurB	Interval
Tenn (N=3)	1492 ± 155	1206 ± 242	0.497 ± 0.03	0.306 ± 0.02	0.04 ± 0.0
Itasca (N=27)	1521 ± 276	1311 ± 521	0.437 ± 0.07	0.302 ± 0.04	0.05 ± 0.0
Mille Lacs (N=9)	1163 ± 401	824 ± 432	0.405 ± 0.07	0.259 ± 0.05	0.04 ± 0.0
Pellston (N=8)	1501 ± 162	637 ± 219	0.512 ± 0.14	0.347 ± 0.04	0.05 ± 0.0
Hope (N=7)	1382 ± 249	663 ± 361	0.445 ± 0.05	0.295 ± 0.03	0.04 ± 0.0
Caro (N=7)	1565 ± 341	1041 ± 718	0.470 ± 0.03	0.330 ± 0.06	0.04 ± 0.0
Halton (N=5)	1733 ± 300	1127 ± 513	0.425 ± 0.11	0.299 ± 0.04	0.04 ± 0.0
Grvhurst (N=8)	1544 ± 204	882 ± 413	0.467 ± 0.09	0.299 ± 0.03	0.04 ± 0.0
Vermont (N=3)	----------	----------	0.416 ± 0.08	0.261 ± 0.01	0.05 ± 0.0
Amherst (N=3)	----------	----------	0.472 ± 0.20	0.310 ± 0.06	0.04 ± 0.0
Overall (N=8, 10)	1487 ± 163	961 ± 249	0.454 ± 0.04	0.301 ± 0.03	0.05 ± 0.0
C. V.	(0.11)	(0.26)	(0.07)	(0.09)	(0.11)
P	0.0289*	0.0070**	0.4829	0.0203*	0.4206

Table 3.6. Population means ± SD of amplitude modulation (Hz) variables from Golden-winged Warbler type I songs. Nine males that sang "monotone" songs were excluded from the analysis for AmA and %AmA (n = 71 birds, df = 7, 63) but not from the analysis of AmB or %AmB (n = 80 birds, df = 9, 70). Significance levels are given for differences across locations as determined by ANOVA (n = 80 birds, df = 9, 70) but are not adjusted for the number of separate tests.

	AmA	AmB	%AmA	%AmB
Tenn (N=3)	84 ± 8	162 ± 4	72 ± 12	30 ± 4
Itasca (N=27)	129 ± 39	142 ± 16	58 ± 13	37 ± 12
Mille Lacs (N=9)	144 ± 59	155 ± 30	63 ± 19	56 ± 10
Pellston (N=8)	121 ± 31	146 ± 20	60 ± 9	52 ± 8
Hope (N=7)	141 ± 33	148 ± 17	63 ± 4	55 ± 10
Caro (N=7)	120 ± 20	144 ± 9	59 ± 10	37 ± 11
Halton (N=5)	134 ± 20	154 ± 6	66 ± 9	41 ± 9
Grvhurst (N=8)	128 ± 17	152 ± 19	56 ± 12	46 ± 10
Vermont (N=3)	----------	144 ± 20	----------	53 ± 7
Amherst (N=3)	----------	138 ± 16	----------	43 ± 7
Overall (N=8, 10)	125 ± 19	148 ± 7.2	62 ± 5.1	45 ± 8.8
C. V.	(0.15)	(0.05)	(0.08)	(0.20)
P	0.3928	0.5959	0.6604	0.0000***

Table 3.7. Locations that differed significantly in pairwise t-tests for Golden-winged Warbler type I song variables. Significance levels were adjusted for the number of pairwise comparisons using the Bonferroni multiple comparison procedure (* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$). Only those variables are shown that had significant location effects as revealed by ANOVA.

	Locations
A phrase variables:	
MaxA	Tenn. vs Itasca*, Hope*, and Caro*
FrA	Tenn. vs Mille Lacs*, Hope**, and Gravenhurst*
B phrase variables:	
PeakB	Itasca vs Mille Lacs*, Hope*, and Gravenhurst*
phrase frequency differences:	
Fdiff	Mille Lacs vs Halton*
Pdiff	Itasca vs Pellston*
amplitude modulation variables:	
%AmB	Mille Lacs vs Tenn.*, Itasca***, and Caro*
	Itasca vs Hope*
temporal variables:	
DurB	Mille Lacs vs Pellston**

Table 3.8. Population means ± SD of frequency (Hz) variables for A phrases from Blue-winged Warbler type I songs. Significance levels are given for differences across locations as determined by ANOVA (n = 65 birds, df = 8, 56) and are not adjusted for the number of separate tests.

Location	MaxA	MinA	MfA	PeakA	FrA
Mur-Han (N=5)	7534 ± 268	5011 ± 484	6272 ± 366	6462 ± 465	2523 ± 276
Columbia (N=8)	7339 ± 533	4635 ± 440	5987 ± 465	6058 ± 692	2704 ± 301
Greer (N=5)	7539 ± 234	5104 ± 477	6322 ± 308	6331 ± 611	2434 ± 429
Hope (N=4)	7352 ± 243	4739 ± 415	6045 ± 319	6090 ± 752	2613 ± 237
Caro (N=3)	7573 ± 314	4819 ± 201	6196 ± 56	6139 ± 247	2754 ± 515
Chelsea (N=9)	7633 ± 117	5073 ± 371	6353 ± 234	6486 ± 491	2560 ± 289
Ithaca (N=6)	7692 ± 446	5254 ± 376	6473 ± 391	6644 ± 579	2438 ± 261
Amherst (N=21)	7856 ± 350	5479 ± 668	6668 ± 489	6793 ± 587	2377 ± 423
E. Mass. (N=4)	7788 ± 288	5231 ± 270	6509 ± 259	6751 ± 442	2557 ± 207
Overall (N=9)	7589 ± 176	5038 ± 270	6314 ± 219	6417 ± 281	2551 ± 125
C. V.	(0.02)	(0.05)	(0.03)	(0.04)	(0.05)
P	0.0268*	0.0143*	0.0088**	0.0842	0.4693

Table 3.9. Population means ± SD of frequency (Hz) variables for B phrases from Blue-winged Warbler type I songs. Significance levels are given for differences across locations as determined by ANOVA (n = 65 birds, df = 8, 56) and are not adjusted for the number of separate tests.

Location	MaxB	MinB	MfB	PeakB	FrB
Mur-Han (N=5)	8247 ± 227	3776 ± 51	6011 ± 121	7184 ± 165	4470 ± 223
Columbia (N=8)	7957 ± 146	3596 ± 239	5776 ± 136	7143 ± 264	4361 ± 288
Greer (N=5)	8158 ± 286	3624 ± 270	5891 ± 136	6995 ± 114	4535 ± 485
Hope (N=4)	8132 ± 124	3633 ± 203	5882 ± 143	7223 ± 118	4500 ± 174
Caro (N=3)	8131 ± 197	3884 ± 150	6007 ± 124	7193 ± 328	4246 ± 246
Chelsea (N=9)	8128 ± 246	3912 ± 294	6020 ± 209	7081 ± 167	4216 ± 346
Ithaca (N=6)	8573 ± 443	4061 ± 347	6317 ± 210	7277 ± 604	4512 ± 676
Amherst (N=21)	7788 ± 333	3568 ± 264	5678 ± 193	6485 ± 785	4039 ±1025
E. Mass. (N=4)	7782 ± 292	3380 ± 275	5581 ± 236	6647 ± 896	4401 ± 317
Overall (N=9)	8099 ± 242	3715 ± 210	5907 ± 217	7025 ± 276	4364 ± 167
C. V.	(0.03)	(0.05)	(0.03)	(0.04)	(0.04)
P	0.0000***	0.0007***	0.0000***	0.0166*	0.7483

Table 3.10. Population means ± SD of frequency (Hz) and temporal (s) variables from Blue-winged Warbler type I songs. Significance levels are given for differences across locations as determined by ANOVA (n = 65 birds, df = 8, 56) and are not adjusted for the number of separate tests.

	Fdiff	Pdiff	DurA	DurB	Interval
Mur-Han (N=5)	260 ± 307	-721 ± 399	0.572 ± 0.10	0.767 ± 0.20	0.04 ± 0.0
Columbia (N=8)	210 ± 436	-1084 ± 778	0.566 ± 0.04	0.607 ± 0.13	0.04 ± 0.0
Greer (N=5)	430 ± 248	-664 ± 614	0.568 ± 0.19	0.686 ± 0.18	0.04 ± 0.0
Hope (N=4)	162 ± 357	-1133 ± 814	0.663 ± 0.15	0.824 ± 0.11	0.04 ± 0.0
Caro (N=3)	188 ± 144	-1053 ± 363	0.605 ± 0.09	0.733 ± 0.06	0.04 ± 0.0
Chelsea (N=9)	333 ± 310	-595 ± 504	0.615 ± 0.08	0.662 ± 0.21	0.04 ± 0.0
Ithaca (N=6)	155 ± 484	-632 ± 966	0.564 ± 0.10	0.752 ± 0.18	0.04 ± 0.0
Amherst (N=21)	989 ± 593	308 ± 1144	0.560 ± 0.09	0.737 ± 0.17	0.03 ± 0.0
E. Mass. (N=4)	928 ± 338	103 ± 1106	0.617 ± 0.05	0.546 ± 0.14	0.03 ± 0.0
Overall (N=9)	406 ± 325	-607 ± 507	0.592 ± 0.03	0.701 ± 0.08	0.04 ± 0.0
C. V.	(0.80)	(0.83)	(0.06)	(0.12)	(0.12)
P	0.0001***	0.0053**	0.6716	0.2728	0.5786

Table 3.11. Population means ± SD of amplitude modulation (Hz) variables from Blue-winged Warbler type I songs. Significance levels are given for differences across locations as determined by ANOVA (n = 65 birds, df = 8, 56) but are not adjusted for the number of separate tests.

	AmA	AmB	%AmA
Mur-Han (N=5)	237 ± 10	42 ± 2	49 ± 11
Columbia (N=8)	231 ± 14	40 ± 3	37 ± 8
Greer (N=5)	230 ± 19	37 ± 2	42 ± 10
Hope (N=4)	238 ± 16	43 ± 2	41 ± 3
Caro (N=3)	229 ± 9	41 ± 3	37 ± 2
Chelsea (N=9)	235 ± 14	42 ± 2	37 ± 5
Ithaca (N=6)	242 ± 11	39 ± 4	33 ± 8
Amherst (N=21)	235 ± 14	41 ± 3	41 ± 13
E. Mass. (N=4)	243 ± 17	40 ± 1	40 ± 14
Overall (N=9)	235 ± 5.0	40 ± 1.8	39 ± 4.5
C. V.	(0.02)	(0.04)	(0.11)
P	0.8056	0.0943	0.3596

Table 3.12. Locations that differed significantly in pairwise t-tests for Blue-winged Warbler type I song variables. Significance levels were adjusted for the number of pairwise comparisons using the Bonferroni multiple comparison procedure. Only those variables are shown that had significant location effects as revealed by ANOVA.

	Locations
A phrase variables:	
MaxA	Amherst vs Columbia*
MinA	Amherst vs Columbia**
MfA	Amherst vs Columbia**
B phrase variables:	
MaxB	Ithaca vs Amherst***, Columbia**, and E. Mass.*
MinB	Ithaca vs Amherst**, E. Mass.**
	E. Mass. vs Chelsea*
MfB	Ithaca vs Amherst***, E. Mass.***, Columbia***, Greer**,
	and Hope*
	Amherst vs Chelsea*** and Murphy-Hanrehan*
	E.Mass. vs Chelsea** and Murphy-Hanrehan*
PeakB	Amherst vs Columbia*
phrase frequency differences:	
Fdiff	Amherst vs Ithaca**, Columbia**, and Chelsea*
Pdiff	Amherst vs Columbia*

Table 3.13. Differences (mean ± SD) in type I song measurements of mixed and non-mixed Golden-winged Warbler populations. Only those variables that differed significantly ($p < 0.05$) when mixed locations were compared to the nearest non-mixed location are shown (paired t-tests, two-tailed). Significance levels are not adjusted for the number of tests.

Golden-wings		Mixed	non-Mixed	P	Mixed group more or less like Bws
Hope, Caro, and Vermont (n = 17) vs all non-Mixed (n = 67):					
		no significant differences			
Hope (n = 7) vs Pellston (n = 8):					
	DurB (s)	0.295 ± 0.33	0.346 ± 0.46	0.0301	less
Caro (n = 7) vs Pellston (n = 8):					
	%AmA	37 ± 11	52 ± 8	0.0106	more
Vermont (n = 3) vs Gravenhurst (n = 8):					
	FrA (Hz)	2770 ± 307	2222 ± 242	0.0120	more

Table 3.14. Coefficients of variation and probability values of Golden-wing type I song measurements of mixed and the nearest non-mixed populations. Only those variables that differed significantly ($p < 0.05$) between groups in Levene's test for homogeneity of variances are shown. Significance levels are not adjusted for the number of tests.

Golden-wings		Mixed	non-Mixed	P
Hope, Caro, and Vermont (n = 17) vs all non-Mixed (n = 67):				
	MaxA (Hz)	0.064	0.044	0.0477
	DurA (s)	0.121	0.215	0.0142
Hope (n = 7) vs Pellston (n = 8):				
	MaxB (Hz)	0.014	0.033	0.0262
	%AmA	0.060	0.163	0.0349
Caro (n = 7) vs Pellston (n = 8):				
	MaxA (Hz)	0.070	0.024	0.0498
	DurA (s)	0.072	0.285	0.0275
	PeakB (Hz)	0.089	0.028	0.0065
	Fdiff (Hz)	0.472	0.107	0.0179
	Pdiff (Hz)	0.819	0.343	0.0028
Vermont (n = 3) vs Gravenhurst (n = 8);				
	Maxa (Hz)	0.116	0.036	0.0104
	MinA (Hz)	0.210	0.026	0.0011
	PeakA (Hz)	0.150	0.030	0.0279
	%AmA	0.103	0.211	0.0485
	MfA (Hz)	0.153	0.029	0.0021
	Fdiff (Hz)	1.400	0.132	0.0030

Table 3.15. Differences (mean ± SD) in type I song measurements of mixed and non-mixed Blue-winged Warbler populations. Only those variables that differed significantly ($p < 0.05$) when mixed locations were compared to the nearest non-mixed locations are shown (paired t-tests, two-tailed). Significance levels are not adjusted for the number of tests.

Blue-wings		Mixed	non-Mixed	P	Mixed group more or less like Gws
Hope & Caro (n = 7) vs all non-Mixed (n = 58):					
	Pdiff (Hz)	-1098 ± 614	-308 ± 1019	0.0499	less
Hope (n = 4) vs Chelsea (n = 9):					
	MaxA (Hz)	7352 ± 243	7633 ± 117	0.0145	less
Caro (n = 3) vs Chelsea (n = 9):					
		no significant differences			
Hope (n = 4) vs Columbia (n = 8):					
	DurB (s)	0.825 ± 0.11	0.607 ± 0.13	0.0211	less
Caro (n = 3) vs Columbia (n = 8):					
	MfB (Hz)	6007 ± 124	5776 ± 136	0.0310	more

Table 3.16. Coefficients of variance and P values of Blue-wing type I song measurements of mixed and the nearest non-mixed populations. Only those variables that differed significantly ($p < 0.05$) between groups in Levene's test for homogeneity of variances are shown. Significance levels are not adjusted for the number of tests.

Blue-wings		Mixed	non-Mixed	P
Hope & Caro (n = 7) vs all non-Mixed (n = 58):				
	%AmA	0.085	0.266	0.0248
Hope (n = 4) vs Chelsea (n = 9):				
	%AmA	0.078	0.146	0.0171
Caro (n = 3) vs Chelsea (n = 9):				
	MaxA (Hz)	0.041	0.015	0.0404
	%AmA	0.067	0.146	0.0089
Hope (n = 4) vs Columbia (n = 9):				
	DurA (s)	0.226	0.082	0.0365
	PeakB (Hz)	0.016	0.037	0.0444
Caro (n = 3) vs Columbia (n = 9):				
		no significant differences		

Table 3.17. Species differences in type II songs. Shown are mean ± SD, sample size, and probability values as determined by t-tests. Hybrids were lumped with the species whose type I song they sang.

Whole song variables	Golden-wing (N)	Blue-wing (N)	P
Peak frequency (Hz)	5893 ± 863 (31)	5716 ± 797 (41)	0.3728
Duration (s)	1.53 ± 0.238 (53)	1.35 ± 0.228 (45)	0.0002
No. of syllables	10.5 ± 2.2 (59)	10.7 ± 2.6 (46)	0.5881
No. of syllable types	3.8 ± 0.74 (59)	2.8 ± 0.65 (46)	0.0000
G syllable variables	**Golden-wing (N)**	**Blue-wing (N)**	**P**
Maximum freq. (Hz)	6751 ± 819 (54)	8216 ± 797 (45)	0.0000
Minimum freq. (Hz)	3814 ± 527 (54)	4022 ± 499 (45)	0.0483
Mean freq. (Hz)	5283 ± 579 (54)	6119 ± 536 (45)	0.0000
Peak freq. (Hz)	4994 ± 684 (54)	5880 ± 1053 (45)	0.0000
Freq. range (Hz)	2936 ± 745 (54)	4194 ± 788 (45)	0.0000
AM rate (Hz)	64 ± 49 (54)	58 ± 16 (44)	0.4194
Duration (s)	0.480 ± 0.108 (54)	0.428 ± 0.09 (45)	0.0126

Table 3.18. Results of sorting type II songs into groups based on similarity of syllable content and structure by four "blind" judges. Values shown indicate the percentage of songs from each geographic location that judges assigned to the same group and, in parentheses, the number of song groups into which judges split each location. At the bottom are given the total number of song groups (with ≥ 2 birds) each judge made from the entire sample of 98 songs, and the number of those groups that were geographically pure (i. e. consisted of birds from a single location).

	% songs correctly grouped (# of groups)				mean %
Location (N)	Judge A	Judge B	Judge C	Judge D	
Itasca (32)	87 (2)	87 (2)	81 (4)	87 (2)	86
Mille Lacs (2)	100 (1)	100 (1)	100 (1)	50 (2)	88
Luttchen Woods (3)	100 (1)	100 (1)	100 (1)	100 (1)	100
Columbia (8)	100 (1)	100 (1)	75 (2)	100 (1)	94
Greer (4)	75 (2)	75 (2)	75 (2)	75 (2)	75
Tenn. (2)	100 (1)	100 (1)	100 (1)	100 (1)	100
Hope (8)	50 (4)	50 (3)	50 (3)	38 (4)	47
Caro (6)	67 (2)	50 (3)	33 (3)	33 (3)	46
Chelsea (3)	67 (2)	100 (1)	67 (2)	100 (1)	84
Gravenhurst (3)	100 (1)	100 (1)	100 (1)	100 (1)	100
Ithaca (3)	100 (1)	67 (2)	67 (2)	100 (1)	84
Vermont (2)	100 (1)	100 (1)	100 (1)	100 (1)	100
Amherst (21)	95 (2)	95 (2)	95 (2)	90 (2)	94
# of groups made from entire sample	12	10	14	11	
# of geographically pure groups	7	5	6	7	

Table 3.19. Prevalence of type II syllable types across recording locations. Shown are number of males at each location whose songs contained each syllable type. The order in which locations are listed approximates three north-south transects. Dashes indicate that species was not present at a particular location.

Syllable type:	A1		A2		B		C	
Location (N)	Gw	Bw	Gw	Bw	Gw	Bw	Gw	Bw
Itasca (32)	11	---	7	---	28	---	0	---
Mille Lacs (2)	0	---	0	---	2	---	2	---
Luttchen Woods (3)	---	3	---	0	---	0	---	0
Columbia (8)	0	3	0	0	0	0	1	7
Greer (4)	---	3	---	0	---	0	---	4
Pellston (1)	0	---	0	---	1	---	0	---
Hope (8)	4	1	0	0	3	0	1	0
Caro (6)	2	0	1	0	4	0	0	0
Chelsea (3)	---	2	---	0	---	0	---	0
Tenn. (2)	0	---	0	---	0	---	2	---
Gravenhurst (3)	1	---	0	---	3	---	2	---
Audley (1)	---	1	---	0	---	0	---	0
Ithaca (3)	---	2[a]	---	0	---	0	---	0
Vermont (2)	0	---	0	---	2[a]	---	0	---
Amherst (21)	2	3	0	0	1	0	0	0
W. Mass. (3)	0	2	0	0	1	0	0	2
E. Mass. (2)	---	0	---	0	---	0	---	0
Birds per species:	20	20	8	0	45	0	8	13
Locations per species:	5	9	2	0	9	0	5	3
Total locations:	12		2		9		7	

[a] includes one Brewster's

continued...

Table 3.19. continued.

Syllable types:	D		E1		F1		F2	
Location (N)	Gw	Bw	Gw	Bw	Gw	Bw	Gw	Bw
Itasca (32)	0	---	5	---	27	---	12	---
Mille Lacs (2)	0	---	2	---	2	---	0	---
Luttchen Woods (3)	---	0	---	0	---	0	---	0
Columbia (8)	0	0	0	0	0	0	0	0
Greer (4)	---	0	---	0	---	0	---	0
Pellston (1)	0	---	1	---	0	---	0	---
Hope (8)	3	1	3	1	0	0	0	0
Caro (6)	0	1	5	0	0	0	0	0
Chelsea (3)	---	0	---	3	---	0	---	0
Tenn. (2)	0	---	0	---	0	---	0	---
Gravenhurst (3)	0	---	0	---	0	---	0	---
Audley (1)	---	0	---	1	---	0	---	0
Ithaca (3)	---	3	---	0	---	0	---	0
Vermont (2)	0	---	2[a]	---	0	---	0	---
Amherst (21)	2	18[b]	1	9[c]	0	0	0	0
W. Mass. (3)	0	0	1	0	0	0	0	0
E. Mass. (2)	---	2	---	0	---	0	---	0
Birds per species:	5	25	20	14	29	0	12	0
Locations per species:	2	5	8	4	2	0	1	0
Total locations:	5		10		2		1	

[a] includes one Brewster's
[b] includes two Brewster's and one Lawrence's
[c] includes one Brewster's and one Lawrence's

continued...

Table 3.19 continued.

Syllable type:	G1		G2		G3		H	
Location (N)	Gw	Bw	Gw	Bw	Gw	Bw	Gw	Bw
Itasca (32)	32	---	0	---	0	---	0	---
Mille Lacs (2)	0	---	2	---	0	---	0	---
Luttchen Woods (3)	---	3	---	0	---	0	---	0
Columbia (8)	1	7	0	0	0	0	0	0
Greer (4)	---	4	---	0	---	0	---	0
Pellston (1)	1	---	0	---	0	---	1	---
Hope (8)	4	2	0	0	1	0	3	0
Caro (6)	5	0	0	0	0	1	0	0
Chelsea (3)	---	1	---	0	---	2	---	0
Tenn. (2)	0	---	0	---	0	---	2	---
Gravenhurst (3)	1	---	0	---	0	---	3	---
Audley (1)	---	1	---	0	---	0	---	1
Ithaca (3)	---	3[a]	---	0	---	0	---	0
Vermont (2)	0	---	2[c]	---	0	---	0	---
Amherst (21)	3	18[b]	0	0	0	0	0	0
W. Mass. (3)	1	2	0	0	0	0	0	0
E. Mass. (2)	---	2	---	0	---	0	---	0
Birds per species:	48	43	4	0	1	3	9	1
Locations per species:	8	10	2	0	1	2	4	1
Total locations:	14		2		3		5	

[a] includes two Brewster's
[b] includes two Brewster's and one Lawrence's
[c] includes one Brewster's

Figure 3.1. Map of study sites and recording locations for Golden-winged and Blue-winged Warblers. The two major study sites, Lake Itasca, Minnesota and Amherst, Massachusetts are marked by stars. See Appendix for additional information about each location.

Figure 3.2. Measurement of type I song amplitude modulation variables from oscillograms. Modulation rate was determined by counting the number of sound pulses per second (Hz) in the final half of each phrase. Percentage of modulation was determined by measuring the distance from the peak of a sound pulse to its trough and using the formula given in Methods. a. complete Golden-winged Warbler A phrase (AM rate = 124 Hz) (same male as in Fig. 3.4a). b. 150 ms section from the same Golden-wing phrase. c. complete Blue-winged Warbler A phrase (AM rate = 240 Hz) (same male as in Fig. 3.5a). d. 150 ms section from the same Blue-wing phrase.

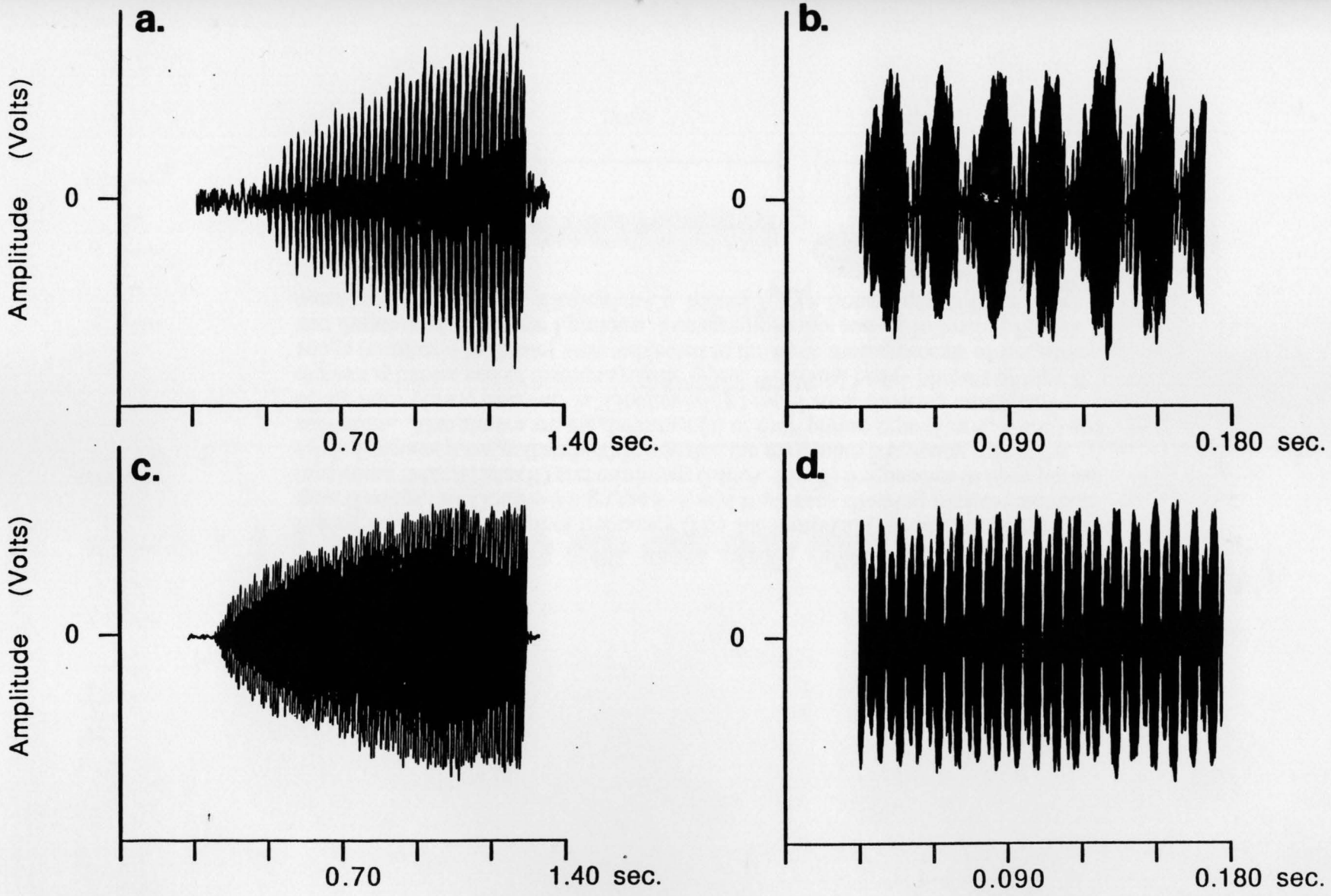

a.
b.
c.
d.
Amplitude (Volts)
0
0.70
1.40 sec.
0.090
0.180 sec.

Figure 3.3. Measurement of frequency (Hz) and temporal (s) variables of type I and type II songs. a. Golden-wing type I A and B phrases showing measurement of maximum (MaxA, MaxB) and minimum (MinA, MinB) frequencies of each phrase type. Frequency range (bandwidth) equaled the maximum frequency minus the minimum. Also shown are the durations (s) of each phrase type (DurA, DurB) and of the inter-phrase interval. b. Golden-wing type II song showing number of distinct syllables and of distinct syllable types. Terminal buzzy phrases of type II songs (number 4 in figure) were subjected to the same measurements of frequency and duration as were type I phrases. Sonagrams in this and all following figures were prepared on a Kay Elemetrics Co. Model 7029A Sonagraph (600 Hz filter).

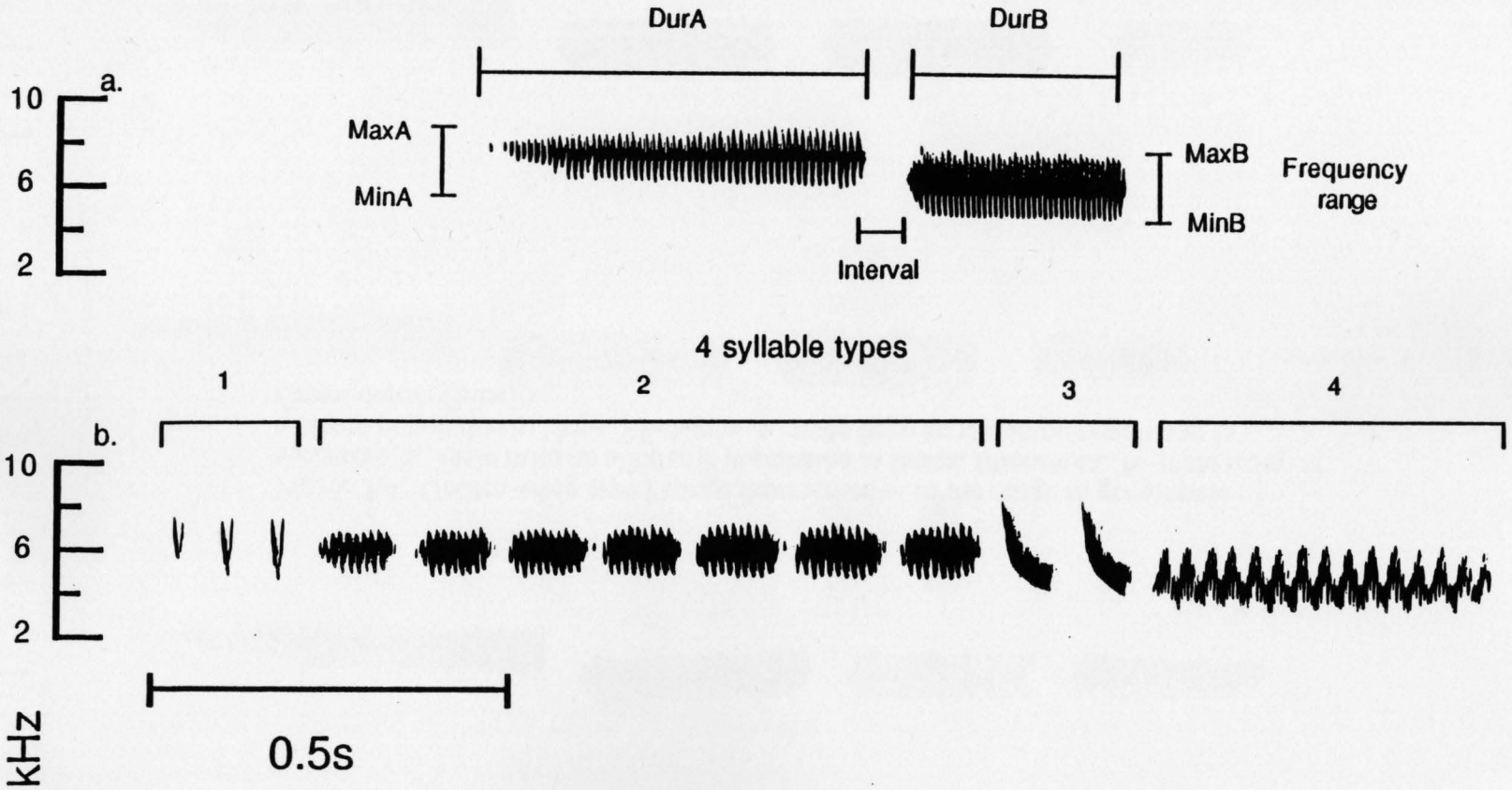

a.
10
6
2
DurA
DurB
MaxA
MinA
Interval
MaxB
MinB
Frequency range
4 syllable types
1
2
3
4
b.
10
6
2
kHz
0.5s

Figure 3.4. Golden-wing type I songs representative of the range in geographic variation. a. male from an allopatric population in Itasca, Minnesota. b. male from a mixed population in Hope, Michigan. c. male from an allopatric population in Gravenhurst, Ontario.

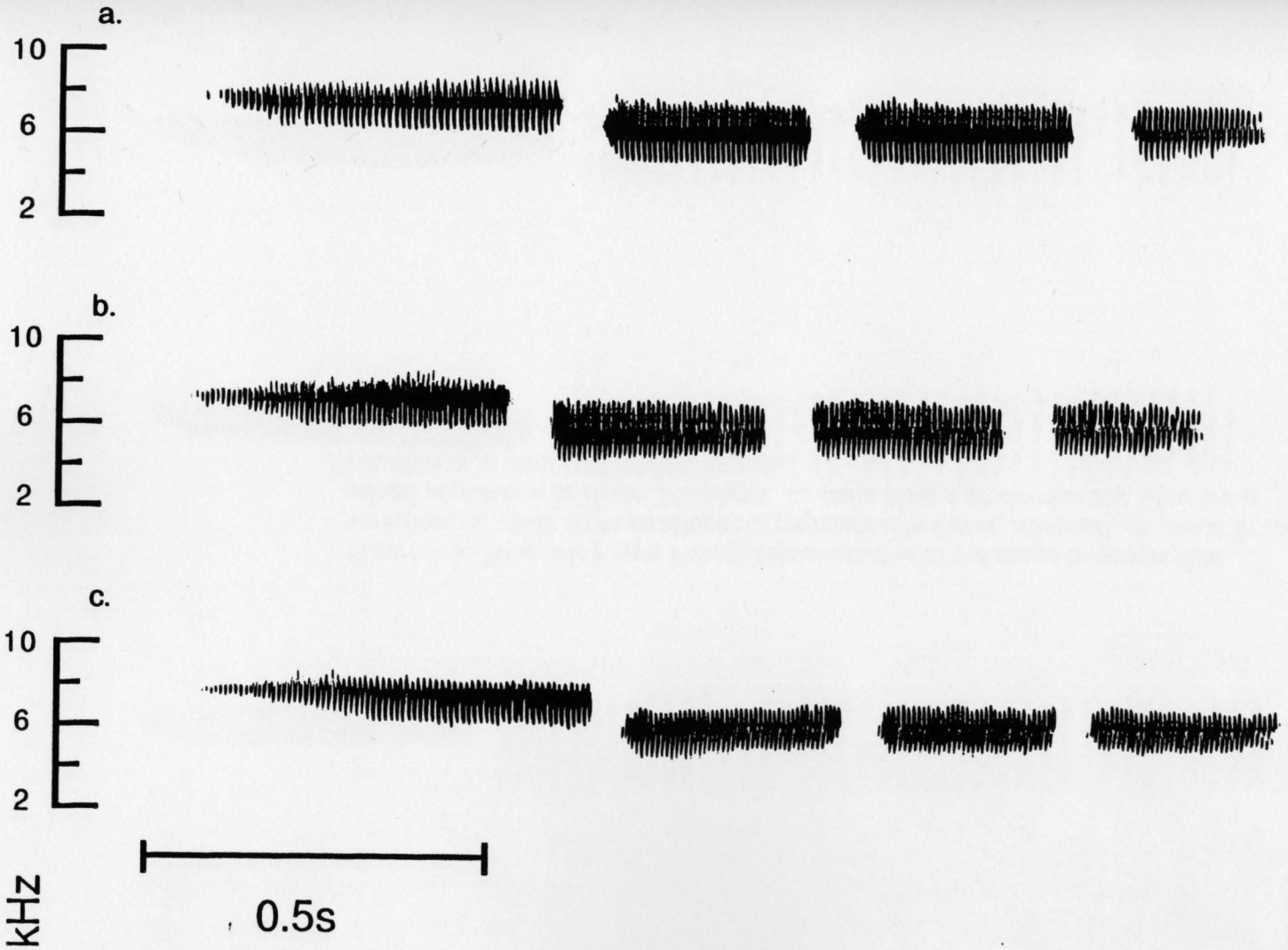

a.
10
6
2
b.
10
6
2
c.
10
6
2
kHz
0.5s

Figure 3.5. Blue-wing type I songs representative of the range in geographic variation. a. male from an allopatric population in Greer, Missouri. b. male from a mixed population in Hope, Michigan. c. male from a predominantly Blue-wing population in Amherst, Massachusetts.

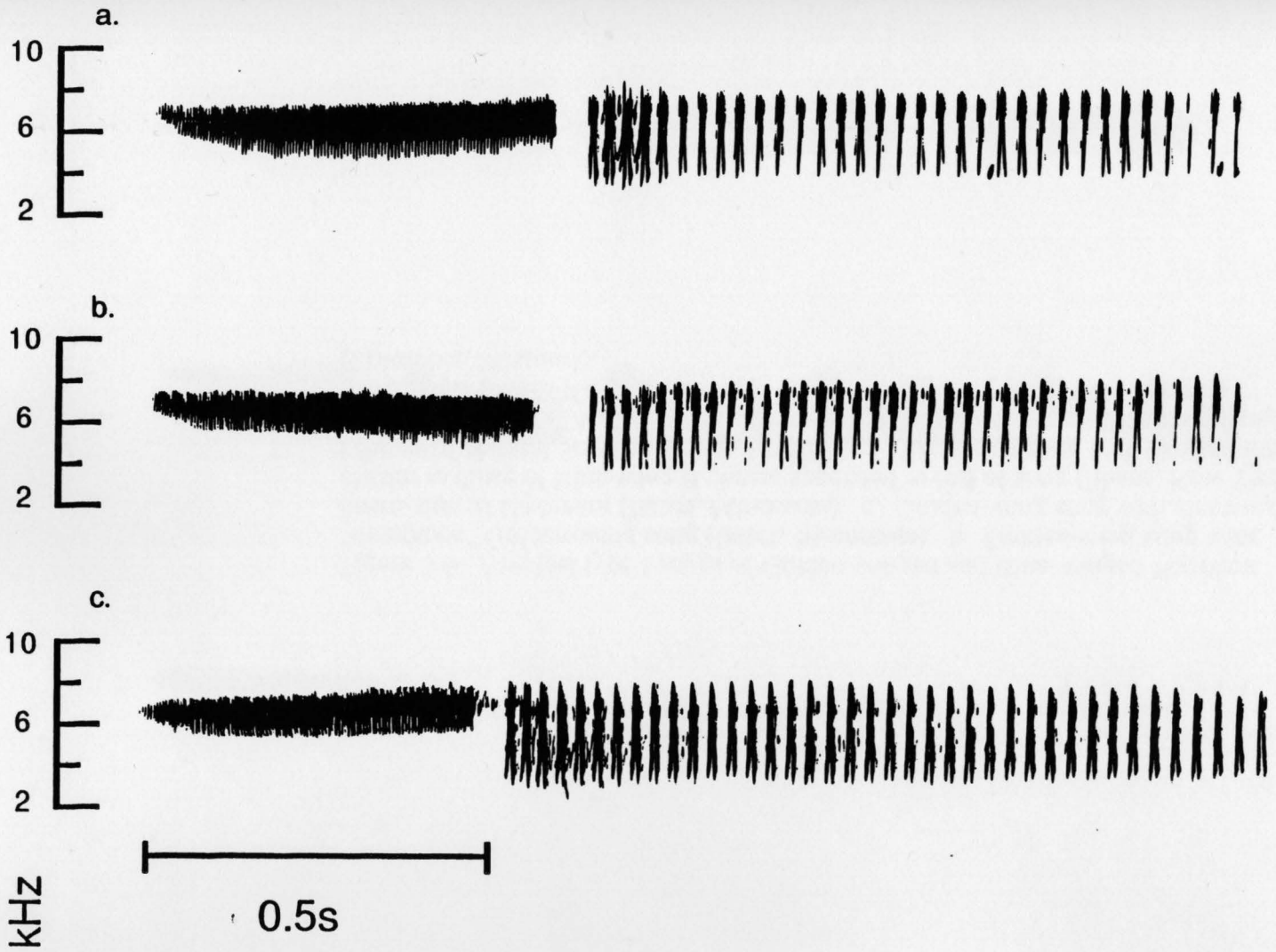
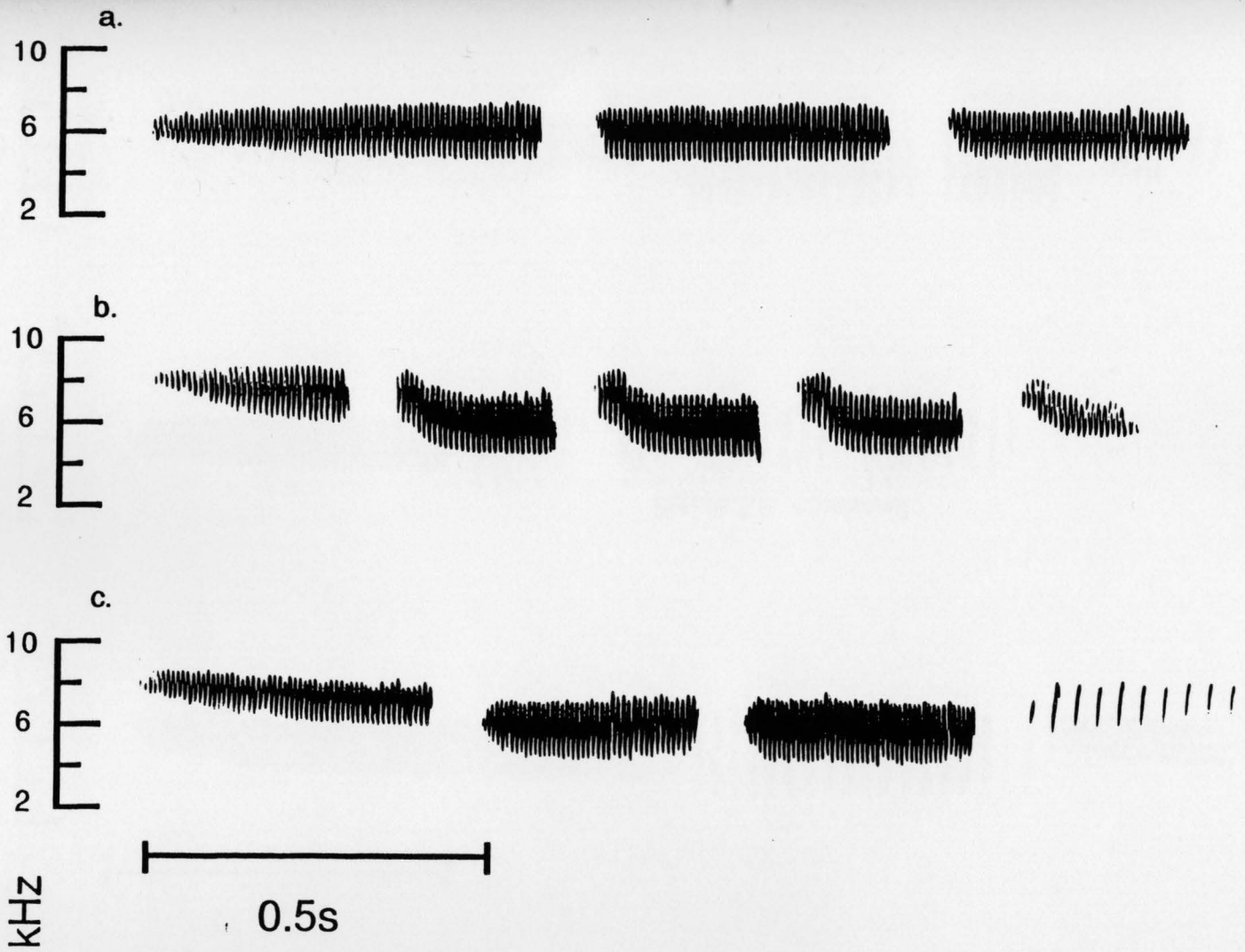

a.
10
6
2
b.
10
6
2
c.
10
6
2
kHz
0.5s

Figure 3.6. Atypical type I songs of Golden-winged and Blue-winged Warblers. a. "monotone" Golden-wing song (Itasca, Minnesota). b. Golden-wing song with down-slurred B phrases (Itasca, Minnesota). c. Golden-wing song with elements similar to those of Blue-wing B phrase appended to end of song (Ithaca, New York, Library of Natural Sounds catalog # 10827). d. Blue-wing song with Golden-wing patterned B phrase (Amherst, Massachusetts). e. Blue-wing song with irregularly patterned B phrase (Greer, Missouri). f. Blue-wing song with A-B-A pattern (Columbia, Missouri).



continued...

Figure 3.6. continued.

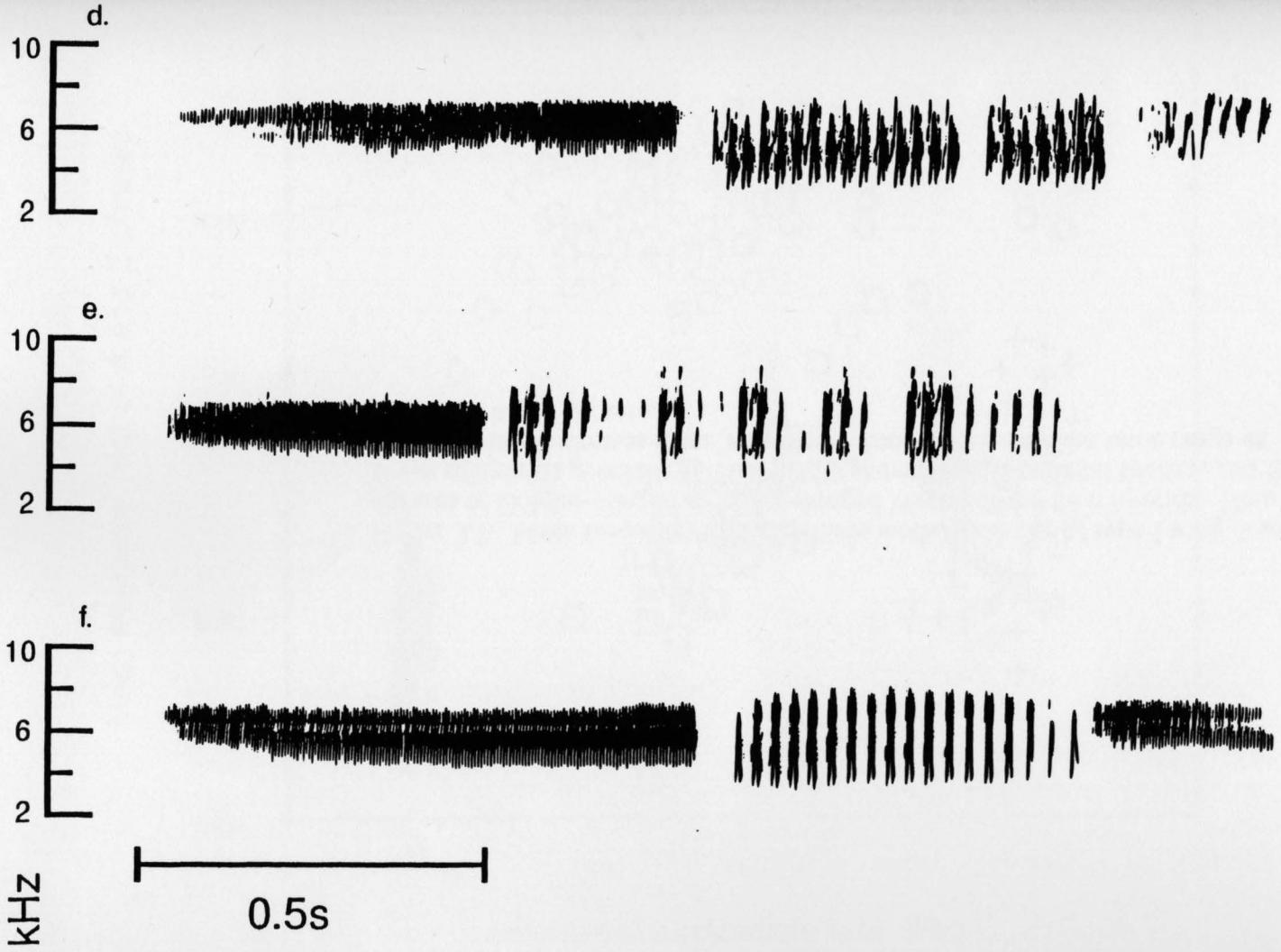

d.
10
6
2
e.
10
6
2
f.
10
6
2
kHz
0.5s

Figure 3.7. Mean frequency and amplitude modulation rate of type I song A and B phrases of Golden-winged and Blue-winged Warblers and their hybrids. Note that songs of hybrids generally fall within the same range as parental species, and that Golden-wing A phrases from "monotone" songs fall within the same range as Golden-wing B phrases.

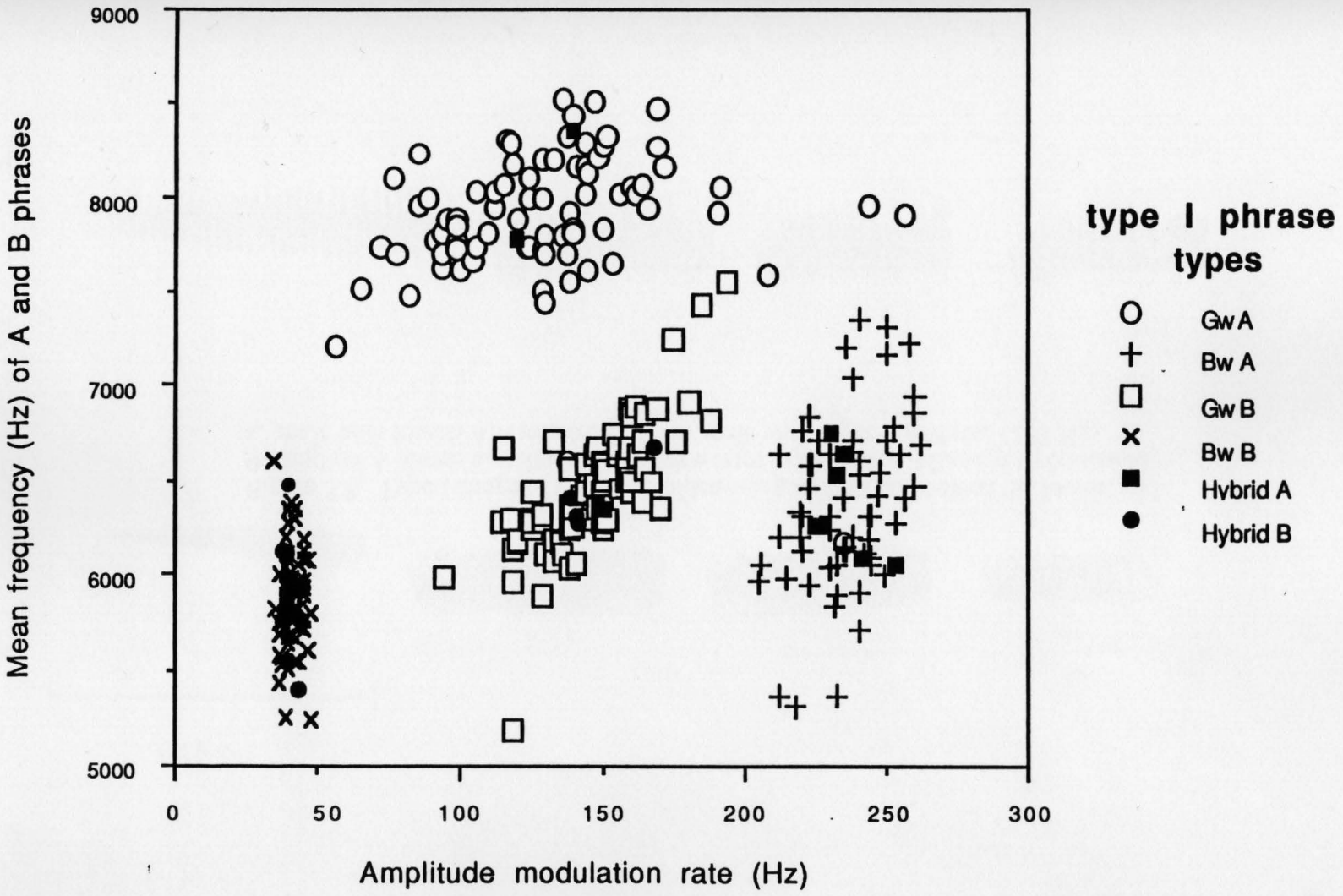

9000
8000
7000
6000
5000
Mean frequency (Hz) of A and B phrases
0
50
100
150
200
250
300
Amplitude modulation rate (Hz)
type I phrase types
Gw A
Bw A
Gw B
Bw B
Hybrid A
Hybrid B

Figure 3.8. Type I songs of the two Golden-wing males that showed the lowest and the highest A phrase amplitude modulation rates in the Itasca, Minnesota population. a. male with lowest AM rate (65 Hz). b. male with highest AM rate (257 Hz).

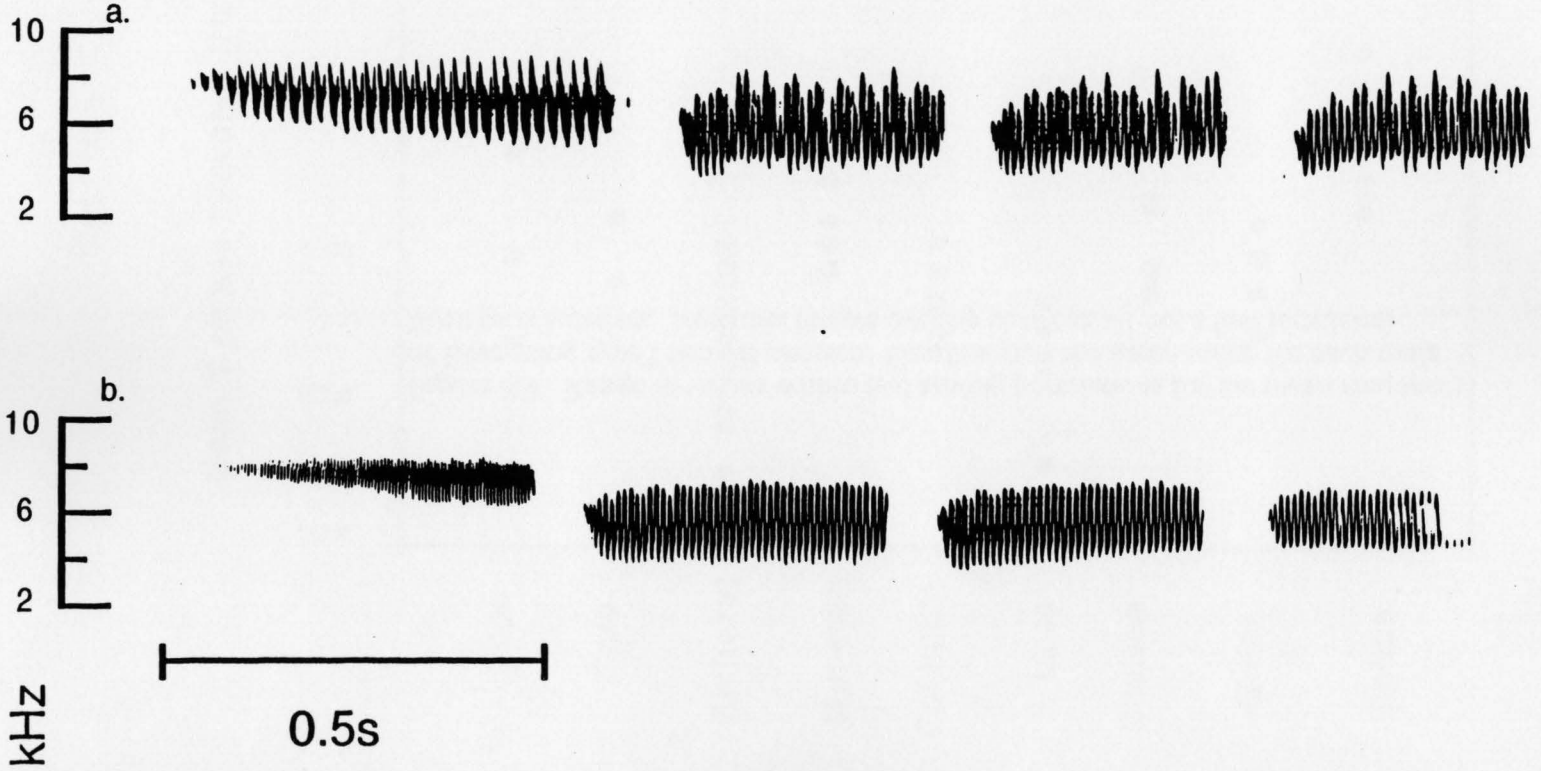

a.
10
6
2
b.
10
6
2
kHz
0.5s

Figure 3.9. Range in values within and among populations for the mean frequency of Blue-wing type I song B phrases. Graph shows the mean value for each male from each location. Note that ranges overlap between all but a few locations.

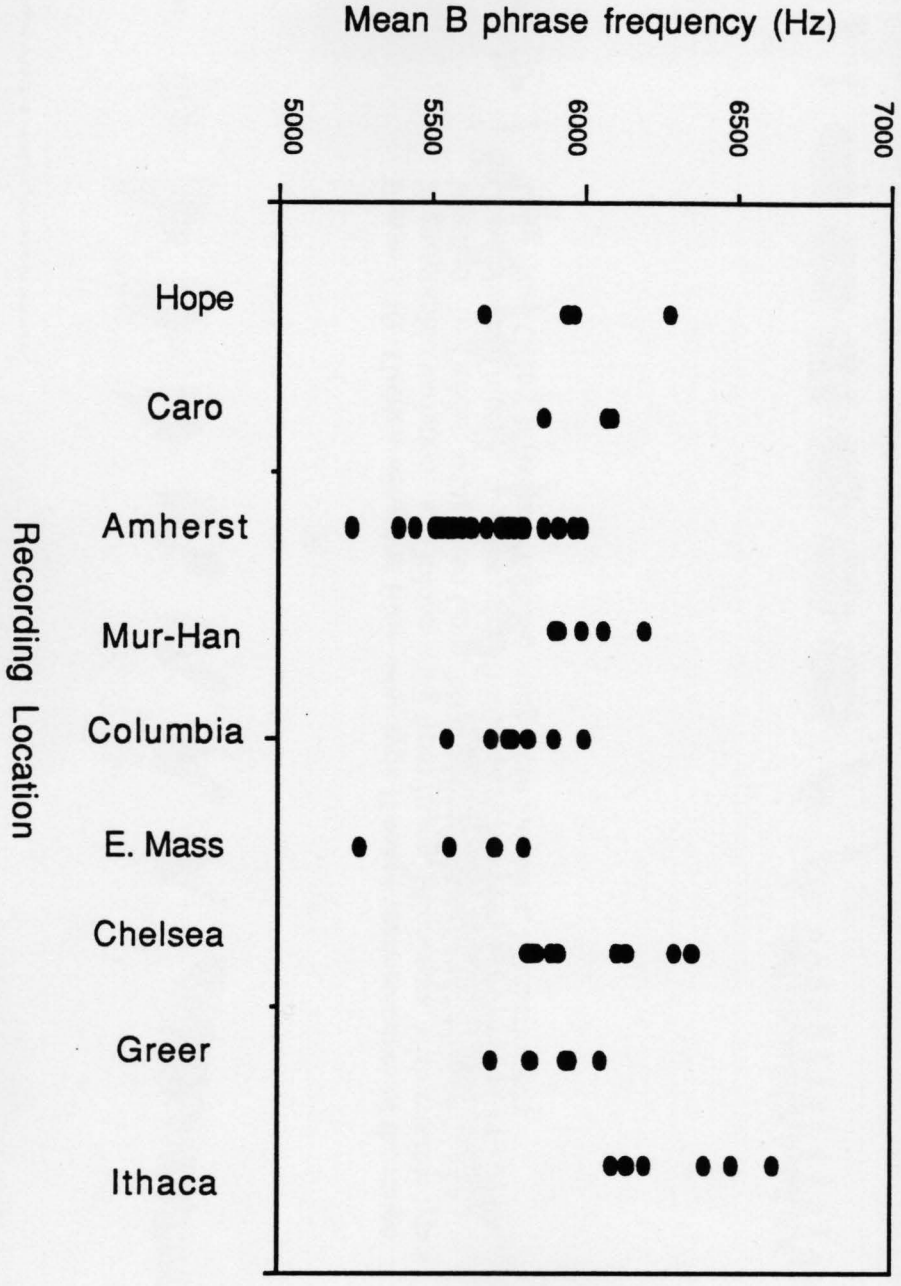
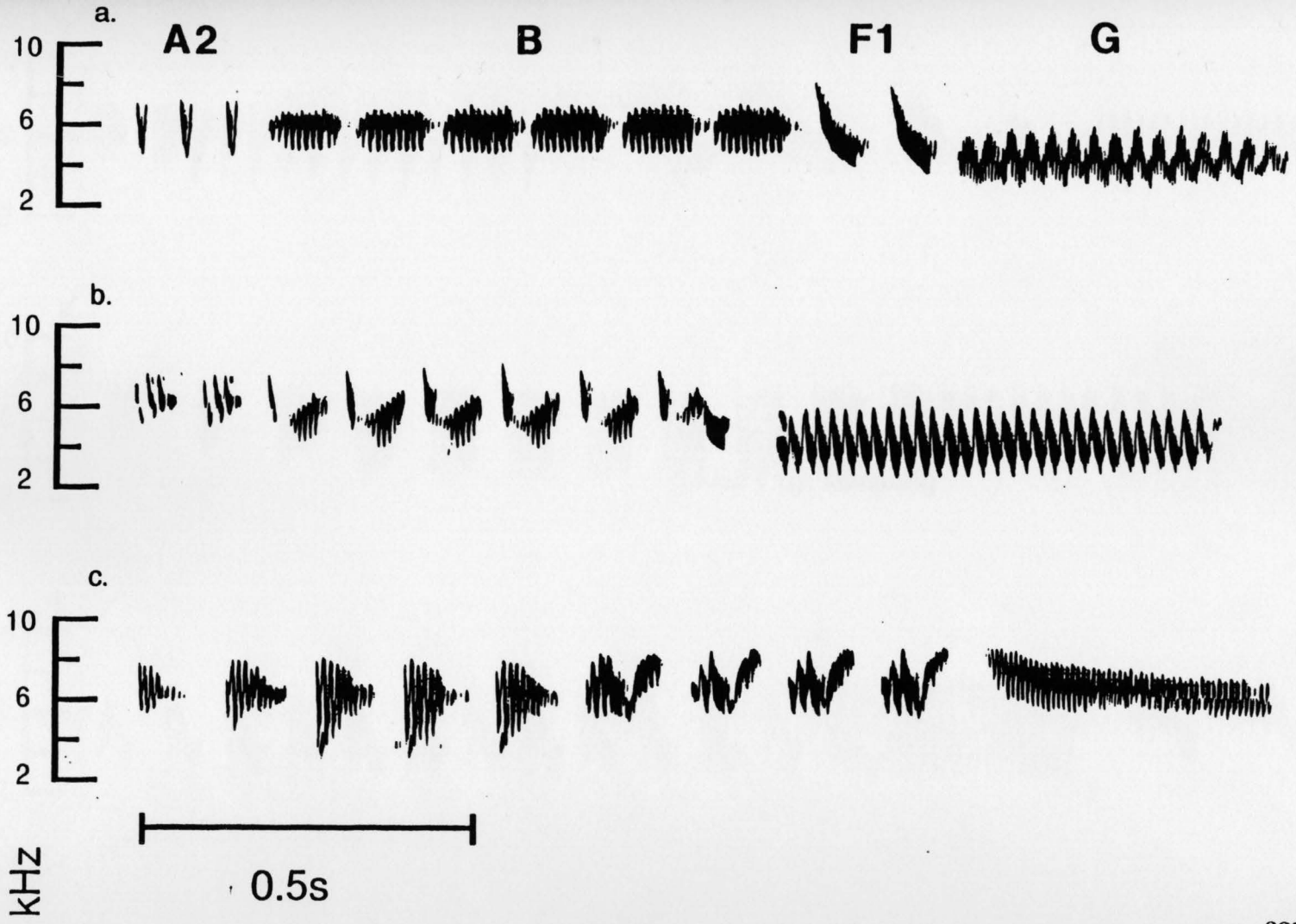

Mean B phrase frequency (Hz)
5000
5500
6000
6500
7000
Recording Location
Hope
Caro
Amherst
Mur-Han
Columbia
E. Mass
Chelsea
Greer
Ithaca

Figure 3.10. Golden-wing and Blue-wing type II songs representative of the range in geographic variation. a. Golden-wing from Itasca, Minnesota, with syllable types labelled. b. Golden-wing from Caro, Michigan. c. Golden-wing from Gravenhurst, Ontario. d. Blue-wing from Luttchen Woods, Minnesota. e. Blue-wing from Greer, Missouri. f. Blue-wing from Amherst, Massachusetts.



continued...

Figure 3.10. continued.

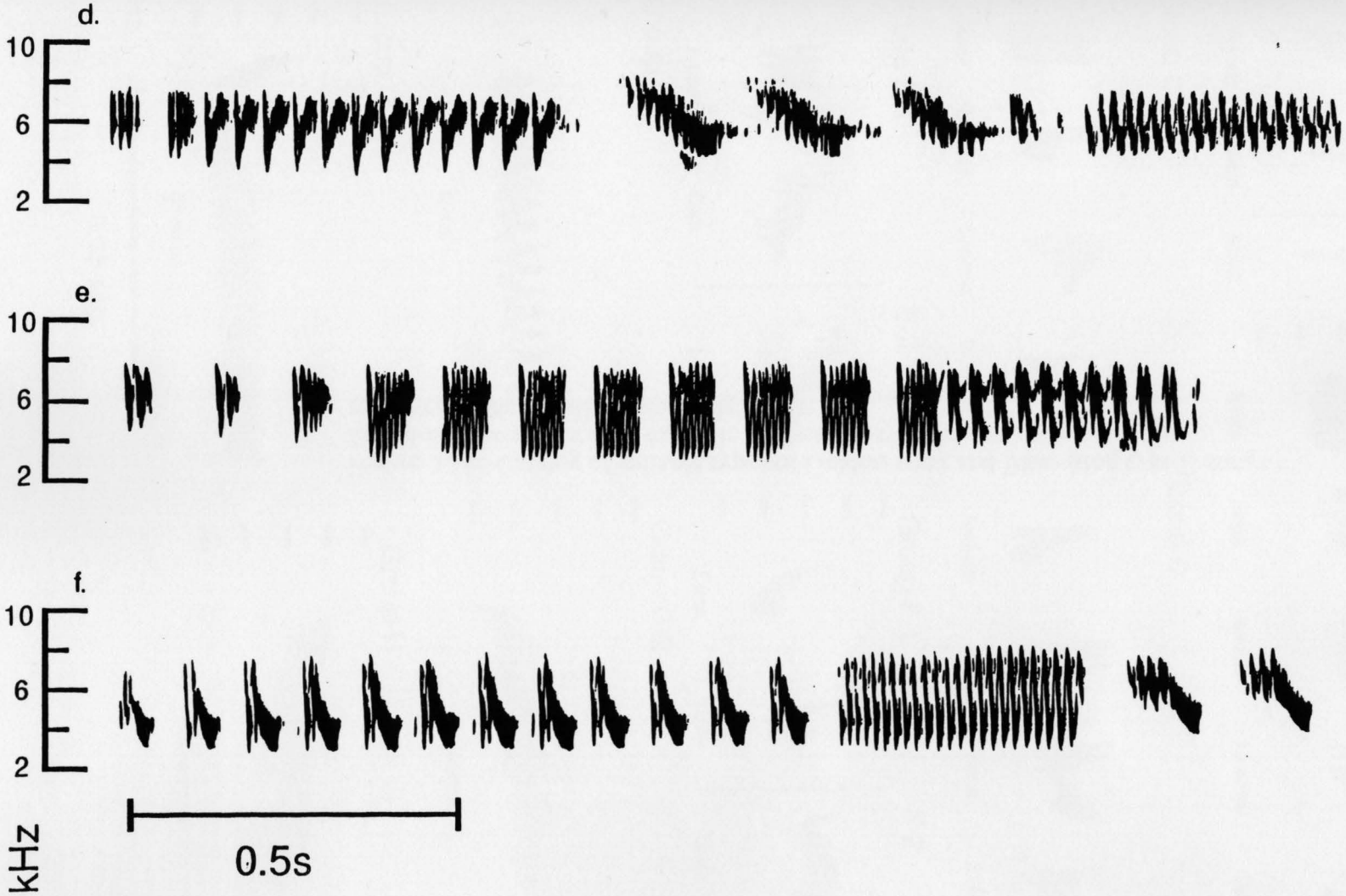

d.
10
6
2
e.
10
6
2
f.
10
6
2
kHz
0.5s

Figure 3.11. Catalog of syllable types of Golden-wing and Blue-wing type II songs. Location of origin for each example is given but syllables are not necessarily restricted to that location (see Table 3.19).

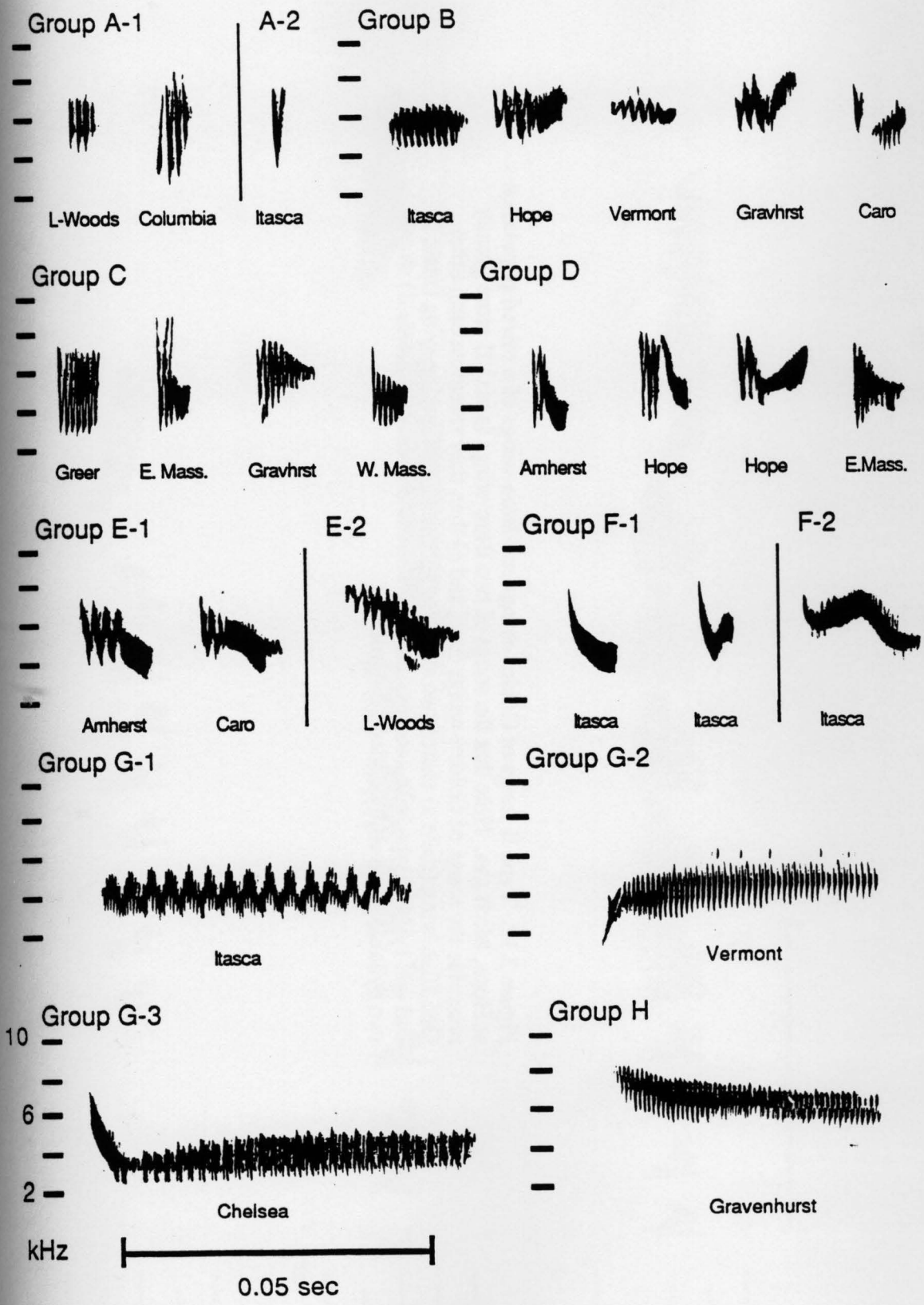
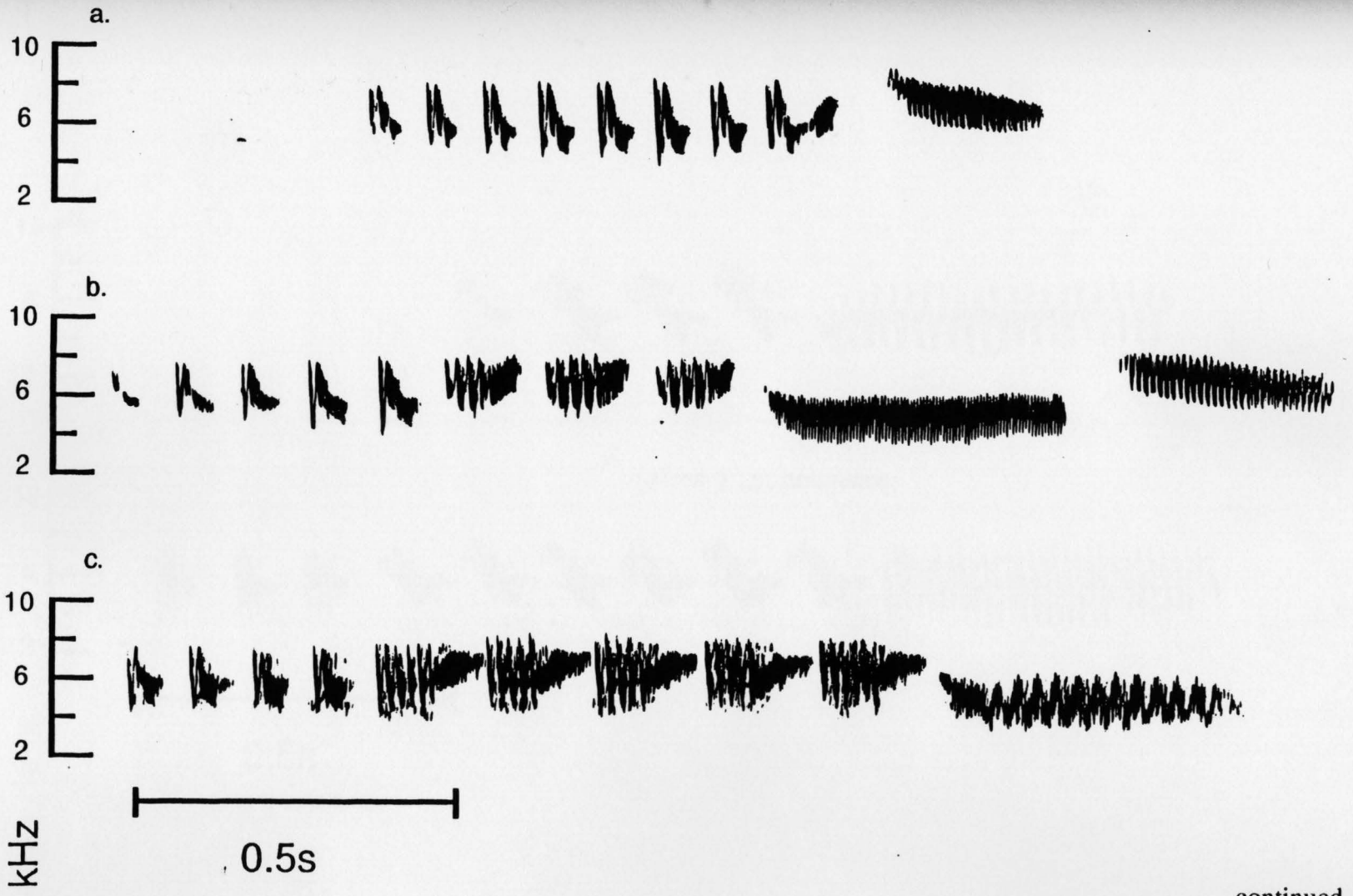

Group A-1
A-2
Group B
L-Woods
Columbia
Itasca
Itasca
Hope
Vermont
Gravhrst
Caro
Group C
Group D
Greer
E. Mass.
Gravhrst
W. Mass.
Amherst
Hope
Hope
E.Mass.
Group E-1
E-2
Group F-1
F-2
Amherst
Caro
L-Woods
Itasca
Itasca
Itasca
Group G-1
Group G-2
Itasca
Vermont
Group G-3
Group H
10
6
2
kHz
Chelsea
Gravenhurst
0.05 sec

Figure 3.12. Type II songs of Golden-wings and Blue-wings of a mixed population at Hope, Michigan. Note that the songs of two Blue-wings (a and d) more greatly resemble the songs of Golden-wings (b, c, and e) than they resemble each other. One Blue-wing (male a) shares two syllable types with one Golden-wing (male b) and one syllable type with another (male c). The other Blue-wing (male d) shares two syllable types with Golden-wing male e.



continued...

Figure 3.12. continued.

kHz
2
6
10
e.
2
6
10
d.
0.5s

CHAPTER 4

SPECIES DISCRIMINATION OF TYPE I AND TYPE II SONGS BY GOLDEN-WINGED AND BLUE-WINGED WARBLERS

The effectiveness of acoustic communication in birds is dependant on the ability of individuals to recognize which among a plethora of ambient vocal signals contains information important to them. As a result, vocalizations containing messages as diverse as those about mating status, territorial status, or even individual identity may be encoded with characteristics that also identify the species of the sender.

A variety of recent studies have used the responses of territorial males to experimentally altered songs to catalog which of the many unique features of a species' song are used to encode species-specific information. Red-winged Blackbirds (*Agelaius phoeniceus*) respond only weakly to songs in which the species-typical trill is greatly shortened or eliminated (Beletsky et al. 1980). The carrier frequency (Bremond 1986) and ordering of syllable types within a song (Kreutzer and Bremond 1986) is important for species recognition in Winter Wrens (*Troglodytes troglodytes*). Alterations of the species-typical shape and duration of notes weakens the response of male Chiffchaffs (*Phylloscopus collybita*) (Becker 1982), and male Veeries (*Catharus fuscescens*) are sensitive to the degree of frequency and/or amplitude modulation within song components (Weary et al. 1986). Work on Field Sparrows (*Spizella pusilla*) by Nelson (1988), and on European Blackbirds (*Turdus merula*) by Dabelsteen and Pedersen (1985), indicates that males are "tuned" to a range of variation in song parameters and are not restricted to only

stereotyped characters for song discrimination. These studies generally support the statement by Becker (1982) that, although a particular character may be especially important, most species use a complex of parameters with supporting or additive effects in species recognition.

Another group of studies has focussed on the abilities of different species, or of different populations within a species, to discriminate between themselves on the basis of acoustical cues found in naturally occurring songs. Red-winged Blackbirds in New York respond more strongly to their local trill than to trills from a California population (Brenowitz 1983). Ratcliffe and Grant (1985) found that two Darwin's finches (*Geospiza fortis* and *G. conirostris*) discriminate against each other's songs as well as against conspecific dialects from other islands. Although sympatric Chiffchaffs and Willow Warblers (*P. trochilus*) maintain mutually exclusive territories, they do not respond aggressively to playback of each other's song (Saether 1983), but sympatric Scarlet (*Piranga olivacea*) and Summer Tanagers (*P. rubra*) do (Shy 1984). Differences in response to heterospecific song between allopatric and sympatric populations of three *Acrocephalus* warbler species were demonstrated by Catchpole (1978).

Relatively few studies have combined the experimental techniques cited above by altering the songs of a particular species so that they more resemble those of a closely related or competing species, and then testing the songs under natural conditions. Emlen (1972), for example, studied species recognition by Indigo (*Passerina cyanea*) and Lazuli Buntings (*P. amoena*), which hybridize where their ranges overlap in the Great Plains. By equalizing the silent intervals between the syllables of each species' song and thus controlling for species-typical differences in cadence, he was able to assess the important role of syllable morphology in eliciting responses from male Indigos (see also Shiovitz 1975). Becker (1982) found that

sympatric Goldcrests (*Regulus regulus*) and Firecrests (*R. ignicapillus*) responded only weakly to playback of normal heterospecific song, but when Goldcrest songs were altered to reduce the frequency contrast between adjacent syllables, Goldcrest responses decreased, and Firecrest responses increased, significantly. Boughey and Thompson (1976) increased the resemblance between Brown Thrasher (*Toxostoma rufum*) and Gray Catbird (*Dumetella carolinensis*) songs by altering the characteristic syllable repetition patterns. Thrashers responded aggressively to the artificial Catbird song, but Catbirds did not respond strongly to the altered Thrasher songs. Other closely related species pairs show similar patterns of response when differences between songs are reduced by alterations of syllable shape and temporal pattern: Wood (*Phylloscopus sibilatrix*) and Bonelli's Warblers (*P. bonelli*), Willow (*Parus montanus*) and Marsh Tits (*P. palustris*) (reviewed in Becker 1982), and Song (*Melospiza melodia*) and Swamp Sparrows (*M. georgiana*) (Peters et al. 1980).

Measuring the responses of males to non-conspecific songs takes on particular biological interest when the species involved interact in complex ways and the experimental alterations of songs mimic the range of variation found in natural populations. I present here the results of such a study on Golden-winged and Blue-winged Warblers. Although they do not maintain mutually exclusive territories (Ficken and Ficken 1968b, Will 1986), Golden-wings and Blue-wings interact extensively and occasionally hybridize in areas where their ranges overlap. Males of both species have repertoires of two stereotyped song types, one of which (type I) is used as a mate attraction signal (Chapter 2, Kroodsma 1988). "Aberrant" type I songs that blend the distinctive characteristics of species typical vocalizations are generally rare but are found in both allopatry and sympatry (see Chapter 3). Little is known about how males of either species react to these atypical songs and whether or not they serve to promote interspecific interactions.

Several previous studies have examined the response of Golden-wing and Blue-wing males to heterospecific type I song. Gill and Lanyon (1964) used two-speaker playback experiments to show that Blue-wing males from an allopatric population in New York clearly discriminated between Blue-wing and Golden-wing songs. One-speaker playbacks done with Blue-wings in sympatric populations in Maryland (Ficken and Ficken 1969), Michigan (Gill and Murray 1972b), and in both sympatric and allopatric populations in New Jersey (Crook 1984), also showed a much reduced response to heterospecific type I. The only one-speaker test of an allopatric Golden-wing population was by Ficken and Ficken (1969) in West Virginia; males responded strongly to conspecific type I songs, but only weakly or not at all to Blue-wing type I. A single study has investigated the response of Golden-wings to experimentally altered type I songs. Ficken and Ficken (1973), working in an allopatric Minnesota population, found that both the A and B phrases were necessary for a strong response and that altering the order and number of phrases in a song generally reduced the level of response.

The results of experiments with type II songs are less clearcut. Both Gill and Lanyon (1964) and Gill and Murray (1972b) found that males responded nearly as strongly to heterospecific as to conspecific type II songs, and in two-speaker experiments with Massachusetts and New York Blue-wings, Kroodsma et al. (1984) suggested that males oriented more closely to conspecific type II songs of the local dialect than to a nonlocal dialect.

I designed experiments to determine the ability of males of both species to discriminate between normal type I songs and type I songs altered to resemble more closely those of the other species. Some of the manipulations of song pattern and frequency (kHz) resulted in experimental songs that were highly similar to atypical

songs recorded in natural populations. I also tested the response of Golden-wing males to Blue-wing type II songs and to a nonlocal Golden-wing type II song.

Methods

Study Sites

All experiments with Golden-wings were performed in the Lake Itasca area of north-central Minnesota, Clearwater and Hubbard Counties, in May and June 1984-1987 (median date 6 June, range 14 May - 26 June). The Itasca population is close to the northwestern edge of the species' range and there is no evidence from plumage characters of genetic introgression with Blue-wings (Gill 1987, pers. obs.). Only two unusual birds, a female Blue-wing and a female hybrid, were noted out of the hundreds of individuals encountered during the course of the study (Highsmith 1987). Although the two species are sympatric as little as 300 km to the southeast, Blue-wings have not been reported to breed in the Itasca area.

Experiments with Blue-wings were performed in or near Amherst, Massachusetts, Hampshire and Franklin Counties, in May and June 1988 (median date 28 May, range 16 May - 3 June). Blue-wings of normal song and plumage predominate in the area but isolated Golden-wings, hybrids, or Blue-wings with aberrant songs occur uncommonly (pers. obs.).

Experimental Procedure and Analysis

Two speakers were placed face up, 20 meters apart on a male's territory with plastic flagging at 4 m intervals between the speakers (Fig. 4.1, p. 138). Experimental tapes consisted of paired song stimuli presented during two 5 min playback periods separated by a 3 min silent intermission. Members of the stimulus pair were played at a natural singing rate (5 songs/min) and alternated between

speakers at about 5 s intervals. Observers stood as far back from the set-up as was practicable (usually about 20 m) and recorded on data sheets the male's position relative to the speakers each time a song was played. The song/speaker orientation was reversed following the intermission. Tapes were played using either Uher 4200 or 4400 Report Stereo IC tape recorders and Olympus SP5 speakers (modified by Mineroff Electronics).

The two-speaker experimental design was chosen because it allowed a male to display an active choice between two stimuli not only by focussing his attention on a particular song/speaker but also by switching his attention from one speaker to the other following intermission. Such a clearcut response necessarily demonstrates discrimination of the two song stimuli by a male, but a negative result can not be assumed to indicate a lack of discrimination. A male may lack the motivation to differentiate between two songs behaviorally even if he is capable of perceiving the differences between them. This design also allows a measure of the relative stimulus value of the two songs and controls for any effects due to order of song presentation or position of speakers on the territory.

The data recorded consist of values (in meters) representing the male's position on a line between the two speakers and 10 m to either side (Fig. 4.1). Because the 10 m areas at the left and right extremes were unmarked, the male's position within them was estimated using the central flagged 20 m as a reference. Data were recorded only when birds were close behind or in front of the 40 m line. Observers (usually two) called out the male's position after each song, while an assistant noted this information on a data sheet along with a running account of the male's vocal activity or other behavior. For experiment 1 only, a single observer recorded this information onto cassette tape and later transcribed it.

Each 5 min playback period contained 25 repetitions of each song, for a total of 50 songs per period and 100 songs per experiment. In relatively few of the experiments were all 100 possible data points recorded. Males required time to locate the playback area once the tape had started, some disappeared during intermission or playback for unknown reasons, and others were distracted by females or other males. Analysis was limited to experiments that yielded a minimum of 20 data points per playback period. Whenever a second male was attracted to the playback area, or something occurred that the observers agreed compromised the focal male's attention, that experiment was aborted.

A small number of the more than 200 Golden-wing males, and 12 of 53 Blue-wing males, were used in more than one experiment, but playback sessions to the same male were separated by at least 10 days. Males that were reused were tested with experimental comparisons they had not previously heard. Cassette tapes of type I or type II songs were often used to attract males to the general playback area before an experiment was started, and were sometimes used to call a male back to the area if it had strayed off during intermission. Because I was testing a male's ability to discriminate between two experimental songs once they were in the playback area, and was not testing the songs' ability to attract males, I do not believe use of this additional tape confounded the results.

For each experimental comparison, I used 1 to 4 experimental tapes with different examples of the songs or song components being compared. For analysis, I determined the median position of a male during each playback period, found the difference between the two periods, and used this single value to represent the result of that experiment. Experiments in which males showed a strong positive response to a particular song (by switching their attention from one speaker to the other after intermission) had values close to $\pm$ 20 m (Fig. 4.2, p. 139). Values for experiments

within a particular comparison were used in the Wilcoxon matched-pairs signed-ranks test (N = number of experiments) to determine significance of difference between males' median positions during the first and second playback periods. Because the Wilcoxon test does not use ties, only experiments with non-zero differences between the first and second playback periods were used in the analysis.

Kroodsma (1989) suggests that the number of replications in experiments comparing classes of songs (e.g. Golden-wing vs Blue-wing type I) should be based on the number of examples of each class used, and not on the total number of experiments to different males. Because I used the total number of experiments within a comparison, and not the number of experimental tapes, to determine the number of replicates (N) for the Wilcoxon test, statistical analysis of responses to the paired song stimuli is confounded by possible differences in response due to the different song examples used on separate tapes. The playback results are therefore presented in a form that displays the range of responses to each tape within a comparison (Fig. 4.2).

Experimental Stimuli: Type I Songs

A wide variety of song stimuli were used in these playback experiments, ranging from normal Golden-wing and Blue-wing type I songs to highly artificial songs composed of elements from both species' repertoires. In general, songs were manipulated in ways that made them more resemble the song of the other species. For example, frequency differences between the A phrases of the two species were eliminated or reversed by raising or lowering the phrases in frequency (Fig. 4.3d - i, pp. 145-147). Species-typical patterns of B phrase endings were altered by merging the separate phrases of Golden-wing endings into a single, long Blue-wing-like phrase or, conversely, chopping up the single, long Blue-wing B phrase into several Golden-wing-like segments (Fig. 4.3b and c, pp. 141-143; Fig. 4.4a, p. 149).

Males generally responded readily to the experimental songs despite their artificial nature, often approaching the speakers closely and perching directly above them. Males also sang in response to playbacks and switched between type I and II songs as they were observed to do in encounters with live conspecific intruders.

Many of the experiments were designed to measure the response of males to song components that differed from each other in only a single frequency or structural parameter. A potential problem in this kind of experiment is that the often subtle differences between songs might elicit responses that would be difficult to evaluate. For example, strong responses by males to a song with an altered A phrase could be due either to lack of discrimination of the altered component or to some overriding stimulus value of the normal B phrase endings. In order to control for this possibility, I further altered the songs in ways intended to focus the males' attention on the component of interest. In experiments that contrasted altered A phrases, for example, I controlled for the stimulus value of normal B phrases by using altered B phrases of presumably neutral stimulus value. In A phrase comparisons with Golden-wings, I substituted the segmented Blue-wing B phrase for the normal Golden-wing B phrases, thus preserving the species-typical pattern of the song ending but changing its structure (Fig. 4.3d). Similarly, in A phrase comparisons with Blue-wings, I substituted a section of Clay-colored Sparrow (*Spizella pallida*) song for the normal Blue-wing phrase (Fig. 4.4b). For B phrase comparisons with Golden-wings, I substituted a raised Blue-wing A phrase for the normal Golden-wing A phrase.

Only recordings of excellent quality were used to make experimental stimuli. Source material included recordings provided by R. D. James from Ontario, D. E. Kroodsma from Massachusetts, W. E. Lanyon from New York, and E. S. Morton from Pennsylvania, as well as recordings made by myself in Minnesota using the

equipment described in Chapter 3. A combination of local and nonlocal songs was used in playbacks to Minnesota Golden-wings, but only nonlocal songs were used in experiments with Massachusetts Blue-wings. Whole songs and song components to be compared were matched for duration and playback amplitude as closely as possible. In general, every attempt was made to make experimental songs within a tape identical except for the phrase or phrases being compared. Final versions of all experimental tapes were prepared using Scotch 209 or 809 recording tape and a Nagra IVS tape recorder.

Artificial songs were prepared by cutting and splicing together components of natural songs, taking care to maintain the inter-phrase intervals of natural songs and to avoid audible "clicks" due to splices. I used a computer based sound analysis system (Zoloth et al. 1980) and sound editing program (EDFFT) to raise or lower song components in frequency. Songs were played into and out of the computer through a Frequency Devices anti-aliasing filter at a sampling rate of 30 kHz. Digitally altered songs were checked against the original analog versions to ensure that both the rate and magnitude of amplitude modulation were preserved. In experiments that compared a raised or lowered song component with an unaltered one, the unaltered component was also digitized to control for effects due to the digitization process.

Experimental Stimuli: Type II Songs

Playback experiments involving type II songs were performed with Minnesota Golden-wings only. Song comparisons contrasted local and non-local Golden-wing songs with each other and with Blue-wing type II songs (Fig. 4.5, p. 151). As above, songs were matched as closely as possible for recording quality and playback amplitude. Because only a limited sample of non-local songs was available,

some non-local songs were used in several different comparisons (Fig 4.5). Type II songs were not altered in any way for experimental purposes.

Visual Presentation of Results

Because of the variety of manipulations performed upon the type I songs used in these experiments, schematic diagrams of the song stimuli (Fig. 4.6, p. 156) were devised to accompany the graphs of experimental results (Figs. 4.7 - 4.10, pp. 157-160). Occasional reference to the normal Golden-wing and Blue-wing type I songs represented in Figure 4.6 will help the reader to understand in what ways these natural songs were modified for the different experiments. In addition, Table 4.1 (p. 135) presents the actual differences in frequency and amplitude modulation characteristics of modified A phrases.

Results

Type I Experiments With Golden-winged Warblers

Comparison of Normal Type I Songs. I first performed a baseline comparison of normal, non-local Golden-wing and Blue-wing type I songs (Exp. 1, Figs. 4.3a, 4.7). Itasca males clearly responded more strongly to conspecific type I songs, with only a single male responding slightly positively to Blue-wing song.

Song Pattern and B Phrase Comparisons. Next I tested the importance of the normal Golden-wing B phrase pattern in song discrimination. The normal B phrases were contrasted with a single long phrase made by splicing together normal B phrases from the same male and removing the inter-phrase intervals (Fig. 4.3b). The artificial B phrases in both tapes were two to three times longer than the mean duration of single B phrases measured in the Itasca population. The phrases were closely

matched for duration in tape 1, but in tape 2 the artificial phrase was 0.06 s, or 8%, longer than the normal phrases.

Males did not show a strong tendency to orient toward the natural phrases in response to either experimental tape, and the responses to the separate tapes differed (Exp. 2, Fig. 4.7). Five of 8 males (62%) oriented toward the normal phrases in tape 1, but 6 of 7 males (86%) oriented toward the artificial phrase in tape 2. It is possible that the greater duration of the artificial phrase in tape 2 may have given it stronger stimulus value than the normal phrases.

The normal pattern relationship between Golden-wing and Blue-wing type I endings was reversed in the next comparison. Single long Golden-wing B phrases (the same phrases used in Exp. 2) were contrasted with Blue-wing B phrases altered to imitate the normal Golden-wing pattern (Fig. 4.3c). The B phrases in tape 1 were closely matched in duration, but in tape 2 the artificial Blue-wing phrases were about 0.14 s, or 15%, longer than the Golden-wing phrase. Males showed a strong orientation toward the long Golden-wing phrase in both tapes (Exp. 3, Fig. 4.7).

A Phrase Comparisons. The following experiments were designed to test males' responses to songs in which discrimination cues were reduced to differences in the mean frequency and amplitude modulation rate of the A phrases. All songs used had identical control endings composed of Blue-wing B phrase elements with typical Golden-wing patterning (Fig. 4.3d).

First I examined whether the natural differences between A phrases in frequency and amplitude modulation rate alone gave males sufficient cues for discrimination. I contrasted both normal, undigitized Golden-wing and Blue-wing A phrases and, as a check of the effects of the digitization process, digitized but otherwise unaltered versions of the A phrases (Fig. 4.3d, Table 4.1). Males oriented toward the Golden-wing A phrase in every instance, without a single male

responding positively to the Blue-wing phrase (Exp. 4, Fig. 4.8). The magnitude of the responses to the digitized tape did not differ from that to the nondigitized versions.

The consistent difference in A phrase frequency between Golden-wings and Blue-wings should provide a stable discrimination cue. I tested for the ability to discriminate on the basis of frequency alone by examining males' responses to Golden-wing A phrases that had identical amplitude modulation characteristics but differed in frequency. Experiment 5 (Fig. 4.8) compared normal Golden-wing A phrases with the same phrases lowered to Blue-wing frequency (Fig. 4.3e; Table 4.1). The frequency of the lowered phrase was below that of any Golden-wing phrase I have measured, except for those from "monotone" songs. Most males showed a strong orientation toward the normal frequency phrase.

Are Golden-wings also sensitive to differences in frequency when the A phrases are of a much higher than normal amplitude modulation rate? In experiment 6, I compared normal Blue-wing A phrases with the same phrases raised to Golden-wing frequency (Fig. 4.3f; Table 4.1). The altered phrases were shifted above the frequency extremes I have measured for Blue-wings. As above, most males oriented toward the A phrases with normal Golden-wing frequency values (Fig. 4.8).

The results of experiments 5 and 6 suggest that males may always orient toward the higher frequency A phrase. I tested for this possibility by reversing the normal frequency relationship between Golden-wing and Blue-wing A phrases. Blue-wing phrases were raised to the normal Golden-wing frequency and Golden-wing phrases were lowered to the normal Blue-wing frequency (Fig. 4.3g, Table 4.1). As above, phrases were shifted beyond the typical range in mean frequency that I have measured for each species. As a group, males exhibited a wide range of responses, with some individuals orienting strongly to the raised Blue-wing phrase

and others to the lowered Golden-wing phrase (Exp. 7, Fig. 4.9). The response to the Golden-wing phrase was more pronounced for tape 3, but each of the other tapes also elicited a single strong response to the lower frequency phrase. Males clearly did not base their responses on the frequency of phrases alone.

The amplitude modulation rate of A phrases also differs consistently between Golden-wings and Blue-wings and could be used in species recognition. In order to investigate this possibility, I attempted to eliminate the frequency differences between Golden-wing and Blue-wing A phrases and thus to contrast the differences in amplitude modulation rate. Experimental songs were made using Blue-wing phrases raised in frequency to Golden-wing level and Golden-wing phrases lowered in frequency to Blue-wing level. Because limitations in the computer editing process rarely allowed complete equalization of the A phrases in frequency, in some tapes one phrase is slightly higher than the other (Table 4.1).

I first contrasted amplitude modulation rate in A phrases that had been matched in frequency at the normal Golden-wing level (Fig. 4.3h). If males were insensitive to amplitude modulation, there should have been little difference in response to the songs within a comparison. The bulk of the responses do show only a weak orientation toward either song; nevertheless, the majority of males (11 of 16) oriented toward the Golden-wing A phrases (Exp. 8, Fig. 4.9). For tape 3, in which the Blue-wing phrase was about 3% higher than the Golden-wing phrase (but still well within the normal Golden-wing range, Table 4.1), two males responded strongly to the Blue-wing phrase but another male responded almost as strongly to the Golden-wing phrase. No consistent pattern in response to the three tapes, or in response to the degree of difference in frequency, is evident.

I also contrasted amplitude modulation rate in A phrases that were matched at the lower frequency level typical of Blue-wing songs (Exp. 9, Fig. 4.3i). Despite its

atypical frequency, most males oriented toward the Golden-wing phrase (Fig. 4.9). Although the frequency of the Golden-wing phrase was slightly higher than the Blue-wing in three of the four tapes (Table 4.1), responses to the tapes do not appear to correlate with the degree of frequency difference. Tape 4, which had the second greatest difference in frequency between the two phrases (almost 5%), nevertheless elicited the largest number of weak responses.

Type I Experiments with Blue-winged Warblers

I repeated the baseline comparison of normal Golden-wing and Blue-wing type I songs using the same tapes as in Golden-wing experiment 1 (Fig. 4.3a). Only a small number of experiments were performed but, like the Minnesota Golden-wings, Massachusetts Blue-wings exhibited a strong response to conspecific songs (Exp. 10, Fig. 4.10).

Unlike the endings of Golden-wing type I songs, which may vary among renditions in the number of B phrases they contain, normal Blue-wing type I songs usually end with a single, long B phrase. I investigated the role in discrimination of Blue-wing B phrases by contrasting normal Blue-wing songs with those same songs altered to produce endings with the typical Golden-wing pattern (songs began with normal frequency Blue-wing A phrases) (Fig. 4.4a). Unlike the results in the similar experiment with Golden-wings (Exp. 2, Fig. 4.7), the majority of males oriented toward the normal Blue-wing songs, but two males responded strongly to the segmented B phrases (Exp. 11, Fig. 4.10). I discovered subsequent to playback that one of these males had a Blue-wing neighbor that sang an aberrant type I song greatly resembling the artificial experimental song (Chapter 3, Fig. 3.6c). It is possible that the other male had also had experience with similar aberrant songs, although his current neighbors all sang type I songs of normal pattern.

Like Golden-wings, Blue-wings were also able to discriminate between songs in which the only normal elements were the A phrases of the two species. I contrasted normal, undigitized Golden-wing and Blue-wing A phrases in a comparison analogous to Golden-wing experiment 4 (the A phrases used in both experiments are identical). Phrases from the song of a Clay-colored Sparrow were used to create artificial control B phrases of normal pattern and duration but abnormal structure (the sparrow syllables were similar in shape to B phrase syllables, but had a narrower frequency range and a higher repetition rate) (Fig. 4.4b). Although there was a single strong response to the Golden-wing A phrase, the majority of males oriented toward the normal Blue-wing phrase (Exp. 12, Fig. 4.10).

Type II Experiments With Golden-winged Warblers

The results of the type II experiments showed that males were able to differentiate between certain paired type II songs, but whether their responses were based on familiarity with local songs, song differences between the species, or the relative durations of songs is unclear.

In order to determine if Golden-wings discriminated between different type II songs, I contrasted Blue-wing type II songs from Massachusetts and Michigan with local Itasca Golden-wing type II songs. One of the three experimental tapes (tape 3) featured a rare Itasca type II song and the other two featured variants of the song that predominated in the area (Fig. 4.5a, b, c). Only in tape 3 was there a large difference in duration between stimuli; the rare Golden-wing type II song was about 14% longer than the Blue-wing song. The majority of males tested (21 of 33) oriented toward the Golden-wing type II songs (Exp. 13, Fig. 4.11, p. 161), but responses to the rare and common variants differed. Although three males did respond strongly to the rare local variant in tape 3, a greater number of males (6 out of 12 tested) oriented toward the Blue-wing song even though it was considerably shorter.

Because there may be substantial within-species differences among type II songs due to geographic variation (Chapter 3), I compared the only non-local Golden-wing type II song (recorded by W. E. Lanyon in New York, Fig. 4.5d) that was available to me with a common local Itasca variant. The only strong orientations were toward the non-local song, which was about 13% longer in duration (Exp. 14, Fig. 4.11).

Despite the geographic differences among type II songs within a species, males may still be able to recognize species-specific characteristics. Experiment 15 consisted of two tapes in which different Blue-wing songs were compared with the same non-local Golden-wing song used in experiment 14. The songs in tape 2 were closely matched in duration, but the Golden-wing song was about 37% longer than the Blue-wing song in tape 1. The results suggested that the large difference in duration may have had an effect on response; although the responses to tape 2 were evenly divided, every male but one oriented toward the Golden-wing song in tape 1 (Fig. 4.11).

Discussion

The data show that the majority of Golden-wing and Blue-wing males tested discriminated readily between the two species' type I songs, as well as between isolated type I song components that had been subjected to a variety of experimental manipulations. Golden-wing males also showed a tendency to discriminate between type II songs. In the following pages I will assess the roles of different song parameters as discrimination cues, discuss whether all males use these cues in the same way, and describe the variability of the cues used in discrimination. Finally, I

will comment on what the experimental results may reveal about natural interactions between the two species.

Males Clearly Discriminated Between Golden-wing and Blue-wing Type I Songs

Not surprisingly, both Minnesota Golden-wings and Massachusetts Blue-wings responded strongly to conspecific type I song when it was contrasted with that of the other species (Exps. 1 and 10, Figs. 4.7 and 4.10). Similar results have been obtained in other allopatric and sympatric populations (Ficken and Ficken 1969, Gill and Murray 1972b, and Crook 1984), but only Gill and Lanyon (1964) also used a two-speaker experimental design.

Golden-wings and Blue-wings Differed in Their Use of B Phrase Pattern as a Type I Song Discrimination Cue

Blue-wing males showed a tendency to differentiate between songs on the basis of B phrase pattern alone, but Golden-wing males did not. Most Blue-wings oriented toward their normal long B phrase, although a few males responded positively to the artificially segmented B phrases that resembled the typical Golden-wing pattern (Exp. 11, Fig. 4.10). Although Golden-wings were presumably able to hear the difference between their normal repeated B phrases and the single, long artificial phrase, the majority of males were not motivated to orient exclusively toward either signal (Exp. 2, Fig. 4.7).

Golden-wings Used B Phrase Structure as a Type I Song Discrimination Cue

The fine structure (i.e. the frequency and amplitude modulation characteristics) of Golden-wing B phrases may be more important in eliciting a strong response than the species-typical pattern with which they are usually sung. Males oriented much more strongly to atypically long single B phrases with the proper structure than to normally patterned phrases made from Blue-wing elements (Exp. 3, Fig. 4.7). In combination with the results of the B phrase pattern experiments

described above, the data suggest that the species-typical pattern of Golden-wing B phrases adds little to the stimulus value of B phrase structure alone.

Males Discriminated Between Songs on the Basis of Natural Type I A Phrase Structure Alone

Males of both species showed a strong conspecific response when songs consisting of natural Golden-wing and Blue-wing A phrases and artificial control endings were experimentally compared (Exps. 4 and 12, Figs. 4.8 and 4.9), but the results were more clearcut for Golden-wings than for Blue-wings. It is possible that the artificial B phrases made from Clay-colored Sparrow syllables reduced the overall stimulus value of the experimental songs more for Blue-wings than the artificially segmented Blue-wing phrases did for the Golden-wings.

Golden-wings Generally Discriminated Between Altered Type I A Phrases

Two broad patterns emerge from the experiments with Golden-wings in which the normal frequency relationship between the two species' A phrases was altered. First, in every one of these experiments that contained a Golden-wing A phrase (Exps. 5, 7 - 9), more males (68% or 46 out of 68 total, including ties) oriented toward the Golden-wing A phrase than to the Blue-wing A phrase. There thus appears to be both a general ability to discriminate using frequency and amplitude modulation cues, and a tendency to orient toward the phrase of Golden-wing origin. Second, despite this general trend, a small but consistent number of males in each experiment failed to orient toward the "correct" phrase. In experiments 7 - 9 (Fig. 4.9), for example, the range of responses across males included strong orientations toward each of the song stimuli.

Golden-wings Used Frequency Cues to Discriminate Between Altered Type I A Phrases

Golden-wing males were clearly able to discriminate between A phrases on the basis of frequency alone (Exps. 5 and 6, Fig. 4.8), and oriented toward the higher frequency phrase whether amplitude modulation was held constant at either normal Golden-wing (Exp. 5) or normal Blue-wing rates (Exp. 6). Of particular interest is that even songs consisting only of Blue-wing elements elicited strong responses from males when those elements were presented at normal Golden-wing frequency and with normal Golden-wing patterning (Exp. 6).

Nevertheless, raising a Blue-wing A phrase to Golden-wing frequency is insufficient to endow it with a stimulus value equal to a normal Golden-wing phrase. If it were sufficient, the results of experiment 7 (Fig. 4.9), in which the normal frequency contrast between Golden-wing and Blue-wing A phrases was reversed, should have shown an overall orientation to the raised Blue-wing phrase. Instead, the majority of males oriented toward the lowered Golden-wing phrase, suggesting both a flexibility in response to phrase frequency and an ability to discriminate on the basis of amplitude modulation rate.

Golden-wings Used Amplitude Modulation Cues to Discriminate Between Altered Type I A Phrases

When frequency differences between A phrases are all but eliminated, Golden-wing males also display an ability to discriminate on the basis of amplitude modulation alone. Although the bulk of responses showed only a weak orientation when the two species' phrases were equalized at the typical Golden-wing frequency (Exp. 8, Fig. 4.9), males oriented strongly toward the phrase with normal Golden-wing amplitude modulation when the phrases were equalized at the low Blue-wing frequency (Exp. 9, Fig. 4.9).

Additional Cues That May Have Affected Discrimination of Altered Type I A Phrases by Golden-wings

Because neither mean frequency nor amplitude modulation rate appears to have primacy as an acoustical cue, it is tempting to look for other factors that may have affected the experimental results. For example, I did not control for differences in peak frequency (frequency of greatest amplitude) or frequency range (bandwidth) between the A phrases within a comparison. Peak frequency should only make a difference in experiments in which I attempted to equalize mean frequency (Exps. 7 and 8) but, because the peak tends to fall slightly below the mean frequency in Golden-wings and slightly above the mean in Blue-wings (Chapter 3), it is not likely to have changed the relative frequencies of the phrases. Although some paired phrases do differ in frequency range, the overlap between species for this parameter is so great (Chapter 3, Table 3.1) that it is unlikely to be useful in species discrimination.

Do All Males Follow the Same Set of "Rules" for Discrimination of Type I A Phrases?

The most parsimonious explanation of these results is that there is no single set of rules that determines the response of all Golden-wing males to a particular A phrase. Different individuals, or perhaps the same individuals in different situations, appear to lack either the ability to discriminate, or the motivation to behaviorally differentiate, between A phrases that have been experimentally altered. Although the majority of Golden-wing males are able to discriminate differences in both the mean frequency and amplitude modulation rate of A phrases, individuals may use the information from each cue in different ways. While some males may consistently orient toward the higher of two phrases in frequency, others may be biased toward the species typical amplitude modulation rate. Repeated playbacks to a series of

individuals might help to determine if males weighed the cues in different ways and, if so, whether individuals were consistent in their responses.

Golden-wings Discriminated Between Local and Non-local Type II Songs

The results of the type II song experiments with Golden-wings suggest that the degree of familiarity with a particular song, rather than with any species-specific song characters, determined males' responses. Itasca males oriented strongly toward locally common type II songs when they were compared to non-local Blue-wing type II songs, but relatively few males oriented toward a locally rare Golden-wing song (Exp. 13, Fig. 4.11).

Previous studies involving two-speaker playback experiments also suggest that intraspecific differences in type II songs may be as important as interspecific differences. Blue-wing males on Long Island, New York responded equally to Blue-wing and Golden-wing type II songs (Gill and Lanyon 1964), but playbacks to Blue-wings from Massachusetts and New York (populations were about 120 km apart) showed that males oriented more strongly to their local type II songs than to Blue-wing songs from the other population (Kroodsma et al. 1984). The differences in response to type II songs by different populations of Golden-wings and Blue-wings may be analogous to the situation reported by Becker (1982) for Goldcrests. Structural differences between Goldcrest songs increase with distance, and males responded less and less strongly to playback of songs from more and more distant populations.

Unfortunately, I can make no definite claims about the roles of species differences in type II song discrimination because my comparisons of local and non-local Golden-wing songs (Exp. 14, Fig. 4.11), and of Blue-wing and non-local Golden-wing songs (Exp. 15, Fig. 4.11), were confounded by large differences in duration between some of the songs used.

Both Variable and Invariant Cues Were Used in Song Discrimination

In an examination of the songs of several species of European songbirds, Marler (1960) suggested that those features of song that are the least variable will provide the greatest contrast with other species and should be used preferentially in species recognition. This hypothesis was supported by Emlen's (1972) experiments with Indigo Buntings, but Emlen cautioned that males did not necessarily use all the invariant characters of a song in species discrimination. Nelson (1988, 1989) has recently challenged this view and cited in support his own work with Field Sparrows and that of Dabelsteen and Pedersen (1985) on European Blackbirds, which show that males of these species use highly variable song features in species recognition.

Although most of the features used by Golden-wings and Blue-wings in species discrimination show only a low level of within-species variation, at least one feature used by Golden-wings was highly variable (Table 4.2, p. 136). The amplitude modulation rate of Golden-wing A phrases varies over a wide range, but the range of variation is generally quite similar from population to population (Chapter 3). This appears to be a good example of birds being "tuned to the normal range of variation they encounter in conspecific song" (Nelson 1988, p. 175).

Golden-wing B phrases provide an interesting example of a song feature with both stereotyped and highly variable features. B phrase fine structure (mean frequency and amplitude modulation) varies within only narrow limits (Chapter 3, Table 3.1), and is important in determining male response to songs (Exp. 3, Fig. 4.7). Although the repeating pattern of B phrases is, at least to human ears, an even more distinctive feature of Golden-wing type I songs, it does not appear necessary in order to evoke a strong response to song playback (Exp. 2, Fig. 4.7). The difference between these two song parameters is that, though present throughout the species, the B phrase pattern is highly variable within individuals (Chapter 2).

Emlen (1972) has suggested that song features that are variable within the repertoire of a male are often used to convey motivational information. This prediction is borne out by observations that Golden-wings use type I songs as a graded series, with shorter songs (i.e. with fewer B phrases) communicating a more aggressive tendency (Chapter 2). If B phrase structure alone provides males with sufficient cues for species discrimination, B phrase pattern may have developed after the establishment of structural differences between the two species as a way of creating a larger effective intraspecific repertoire.

Does Prior Experience Affect a Male's Response to Songs?

Males that have had agonistic encounters with individuals that sang atypical vocalizations, or who themselves sing unusual songs, may be more likely to respond aggressively to songs that differ from normal in one or more parameters. Rice (1981) reported that the neighbors of a male Red-eyed Vireo (*Vireo olivaceus*) that sang a grossly aberrant song responded strongly to playback of the aberrant song, but males many territories distant responded only to normal song. When Kreutzer (1987) played an atypical song to three different populations of Cirl Buntings (*Emberiza cirlus*), only males from the location where the song was recorded responded as strongly to it as to normal song. At least one of the two strong responses to an abnormally patterned song in this study (Exp. 11, Fig. 4.10) was by a Blue-wing male whose immediate conspecific neighbor sang a very similar aberrant song (Chapter 3, Fig. 3.6c).

Observations of two Itasca Golden-wings with atypical songs suggested that neighboring males responded normally to them. One male that sang a "monotone" type I song (i.e. with an atypically low frequency A phrase) and the locally common type II variant used both song types in counter-singing bouts with other males. The other male's repertoire consisted of the locally rare type II variant and a type I song

that featured an A phrase of normal frequency but with a much higher than normal amplitude modulation rate (about 240 Hz, typical of Blue-wing A phrases). Despite his unusual songs, this individual held the same territory two years in a row and appeared to secure a mate each year.

In contrast, observations by Gill and Murray (1972b) in the mixed population of Golden-wings and Blue-wings they studied in Michigan indicate that males with atypical songs are not always treated as conspecifics by neighbors. The conspecific neighbors of a Blue-wing male that sang a Golden-wing-patterned song (A-A-A) responded only to normal Blue-wing songs. Another bird had Golden-wing plumage but sang a normal Blue-wing type I song. This contrast between heterospecific plumage and conspecific song apparently gave rise to conflicting tendencies in his Blue-wing neighbor. The neighbor initially responded aggressively to this male's song, but stopped responding altogether after several days.

The Role of Song in Interspecific Interactions

Golden-wings and Blue-wings displayed acute skills in discriminating between natural and unnatural songs under highly artificial experimental conditions, but generalizing about how these skills may be used in natural encounters is difficult. Playback experiments that used more naturalistic stimuli might have allowed greater generalization, but much of the information about the specific cues used in song discrimination would have been lost. The results do make it clear that responses to both type I and type II songs are characterized by a large degree of variability among males.

This variability in response to experimentally isolated acoustical cues is likely to translate into even greater variability in natural encounters, when cues about vocal displays are combined with information about visual displays and plumage patterns. Gill and Murray (1972b) performed one-speaker playbacks in a mixed population of

Golden-wings and Blue-wings in Michigan. Almost 20% of the males they tested responded to heterospecific type I song and 68% responded to New York Blue-wing type II. Although two-speaker experiments would be required to test the relative stimulus values of these songs, the results indicate quite variable responses to natural songs.

The results of the present study showed that, in the particular populations tested, normal type I songs are not likely to stimulate interspecific interactions, but songs that mix the structure and pattern of the two species' phrases may well elicit investigatory responses. Type II songs, especially if from a not too distant population, seem more likely to provoke interspecific responses. Agonistic encounters with individuals that sing atypical songs, or that display a mismatch of vocal and plumage characters, may dispose some males toward greater flexibility in response.

Experiments with females are necessary to determine if flexibility in response to songs, or outright errors in discrimination, contributes to the incidence of hybridization. If females are sensitive to the same song parameters that males use in species recognition, normal type I songs, which are used as mate attraction signals (Chapter 2), should serve as an effective reproductive isolating mechanism.

Table 4.1. Frequency and amplitude modulation characteristics of Golden-wing and Blue-wing A phrases used in playback experiments. Also shown are differences between members of each stimulus pair.

		Mean Freq. (kHz)			AM Rate (Hz)		
Exp.	Tape #	Gw	Bw	diff	Gw	Bw	diff
4, 10	1	7.69	6.28	1.41	83	266	183
	2	7.93	6.43	1.50	143	259	116
7	1	6.44	8.16	1.72	83	260	177
	2	6.35	7.30	0.95	121	236	115
	3	6.20	7.37	1.17	136	251	115
8	1	8.16	8.32	0.16	76	223	147
	2	8.40	8.16	0.24	130	207	77
	3	7.93	8.16	0.23	143	260	117
9	1	6.75	6.75	0.00	143	251	108
	2	6.52	6.44	0.08	136	251	115
	3	6.44	6.12	0.32	121	236	115
	4	6.41	6.12	0.29	83	236	153
		Gw	Gw		Gw		
5	1	7.69	6.35	1.34	121		
	2	7.61	6.51	1.10	143		
		Bw	Bw		Bw		
6	1	6.12	7.45	1.33	243		
	2	6.09	7.37	1.28	228		

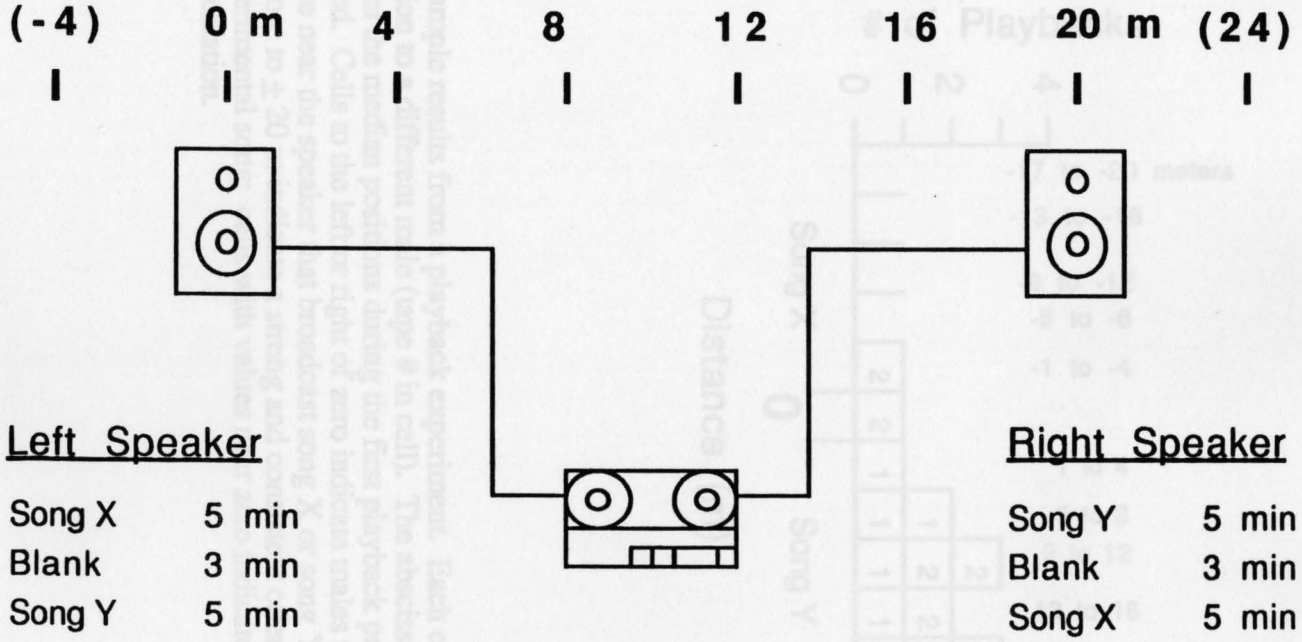
Table 4.2. Within-species variability of type I song features (based on coefficients of variation) and their role in song discrimination as revealed by playback experiments. Data on variability of song features are from Chapter 3.

	Golden-wings		Blue-wings	
song feature	level of variability	used in discrimination?	level of variability	used in discrimination?
B phrase pattern	low[a]	no	low	yes
B phrase structure	low	yes	low	?
A phrase structure:				
mean frequency	low[b]	yes	low	yes
amplitude modulation	high	yes	low	?

[a] highly variable within the repertoire of individual males

[b] small numbers of males within a population may have very low frequency phrases

Figure 4.1. Diagram of two-speaker playback experiment. Speakers were placed 20 m apart on a male's territory with plastic flagging at 4 m intervals between the speakers.



Left Speaker

Song X	5 min
Blank	3 min
Song Y	5 min

Right Speaker

Song Y	5 min
Blank	3 min
Song X	5 min

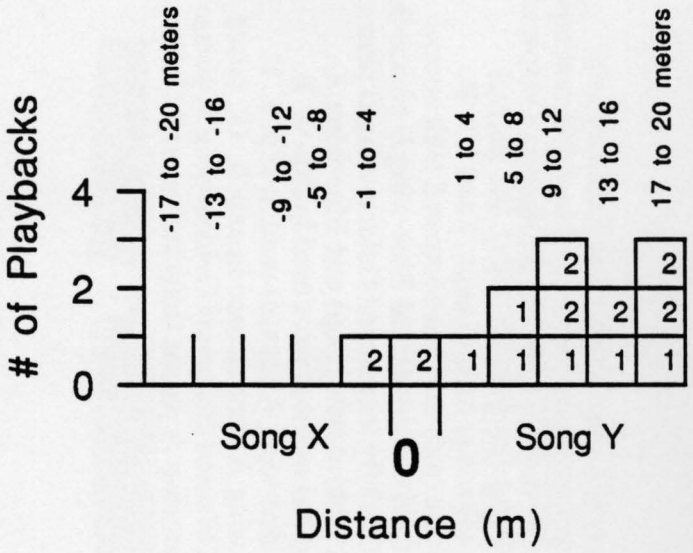
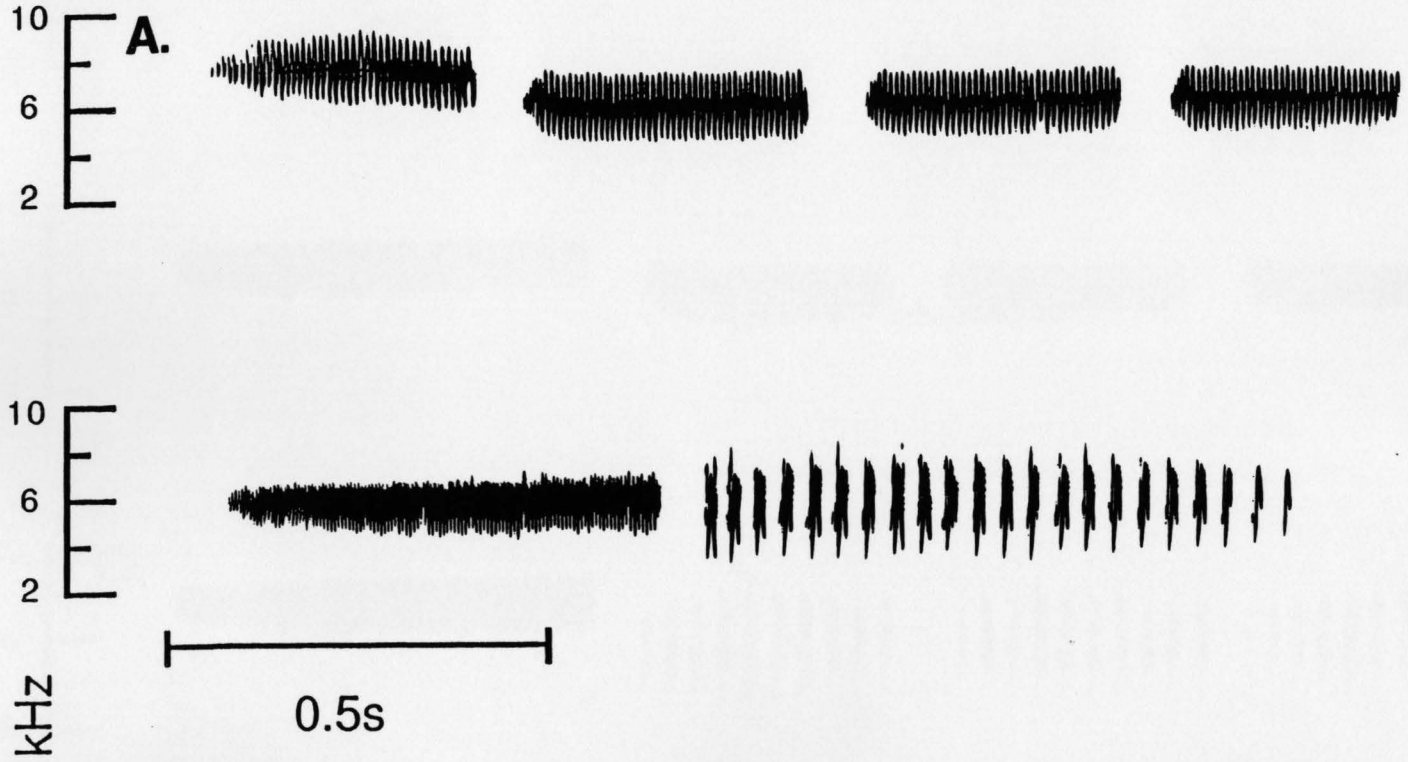


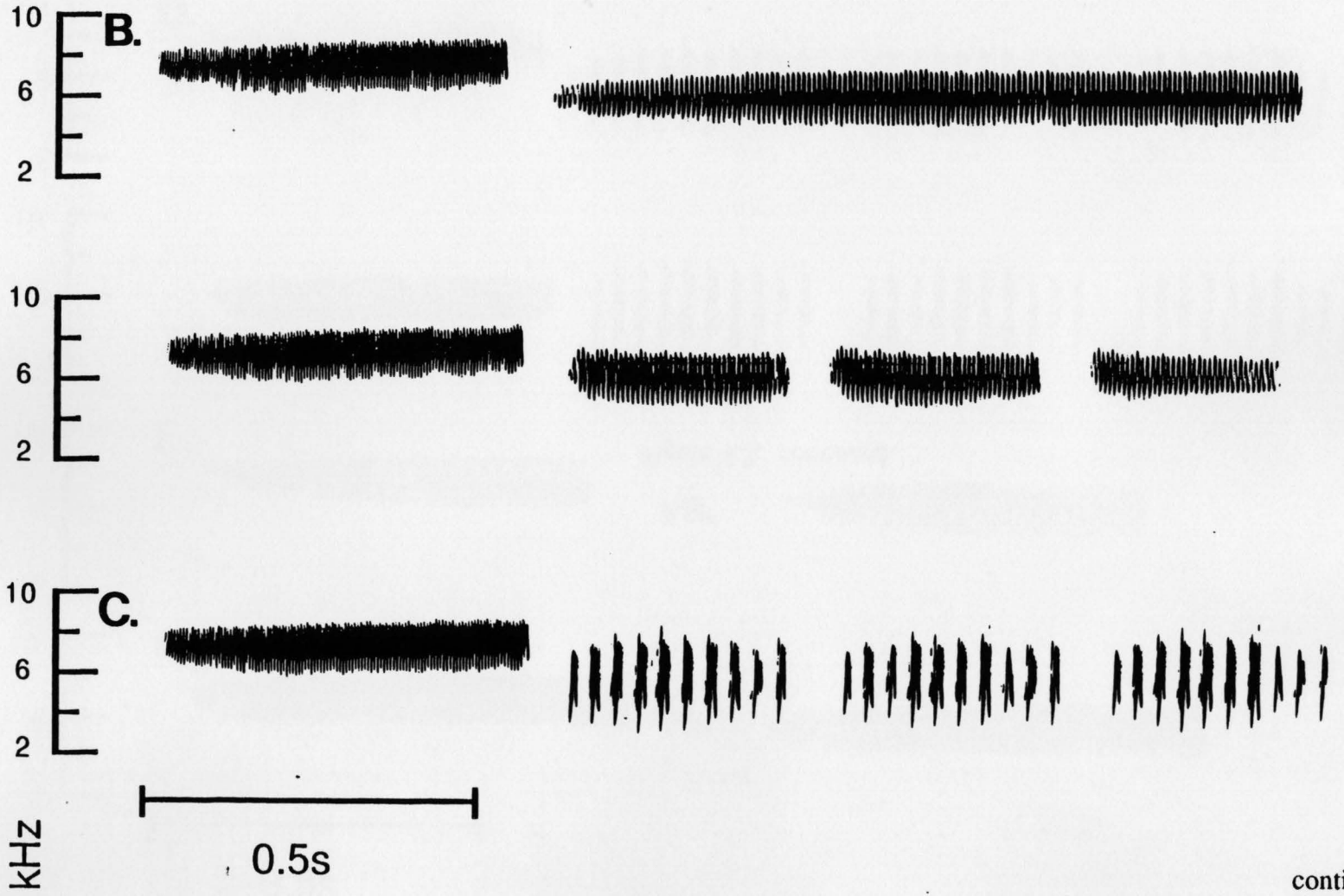
Figure 4.2. Sample results from a playback experiment. Each cell represents a playback session to a different male (tape # in cell). The abscissa is the difference in meters between the median positions during the first playback period and the second playback period. Cells to the left or right of zero indicate males that spent a greater amount of time near the speaker that broadcast song X or song Y, respectively. Cells with values close to $\pm$ 20 m indicate a strong and consistent orientation toward a particular experimental song; cells with values near zero indicate only a weak directional orientation.

Figure 4.3. Experimental stimuli used in type I song playback experiments with Golden-winged Warblers. Shown are examples from one of the 2 to 4 different tapes used in each experiment. Sonograms in this and all following figures were prepared on a Kay Elemetrics Co. Model 7029A Sonagraph (600 Hz filter). A. normal Golden-wing (top) and Blue-wing (bottom) songs used in exps. 1 and 10. B. artificially lengthened Golden-wing B phrase (top) that was compared with normal Golden-wing B phrases in exp. 2. C. artificially segmented Blue-wing B phrase that was compared in exp. 3 with the same artificially lengthened Golden-wing B phrase used in exp. 2 (see b above). D. normal Golden-wing (top) and Blue-wing A phrases coupled with artificial Blue-wing endings that were used in exp. 4. E. normal (left) and lowered frequency Golden-wing A phrases used in exp. 5. F. raised frequency (left) and normal Blue-wing A phrases used in exp. 6. G. raised frequency Blue-wing A phrase (left) and lowered frequency Golden-wing A phrase used in exp. 7. H. raised frequency Blue-wing A phrase (left) and normal Golden-wing A phrase used in exp. 8. I. normal Blue-wing A phrase (left) and lowered frequency Golden-wing A phrase used in exp. 9.



continued...

Figure 4.3. continued.



continued...

Figure 4.3. continued.

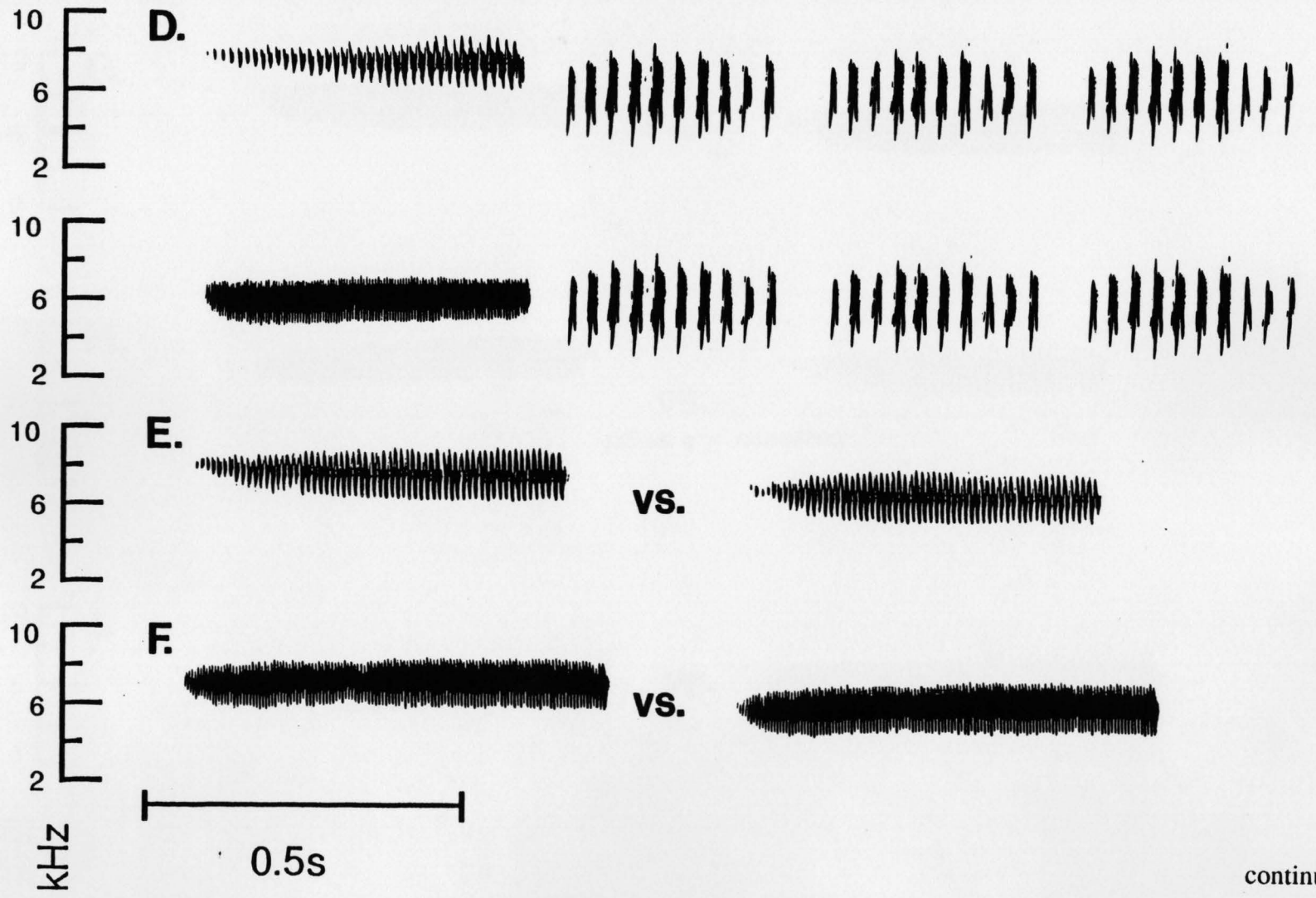


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Figure 4.3. continued.

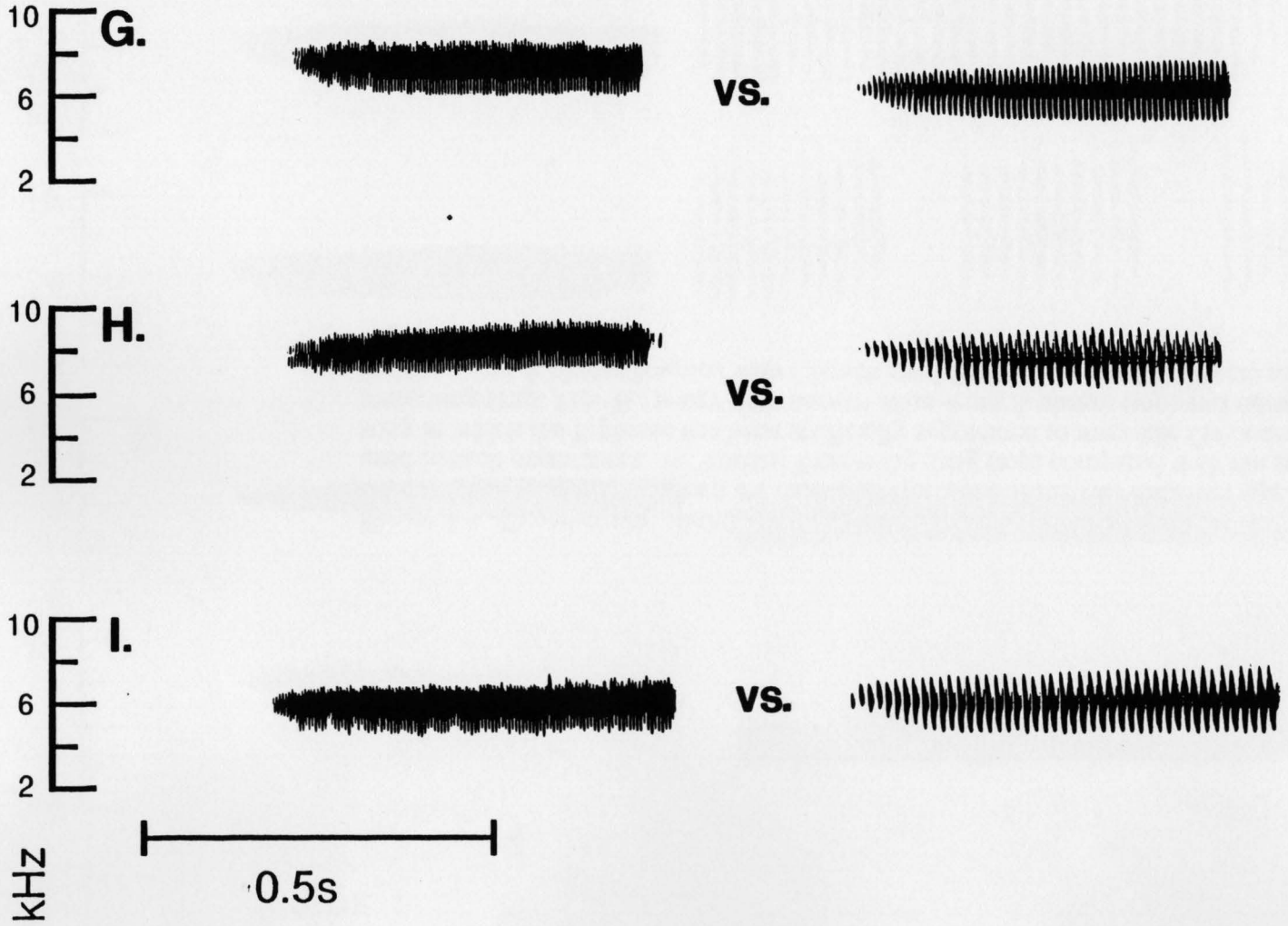

10
6
2
G.
vs.
10
6
2
H.
vs.
10
6
2
I.
vs.
kHz
0.5s

Figure 4.4. Experimental stimuli used in type I song playback experiments with Blue-winged Warblers. Shown are examples from one of the two different tapes used in each experiment. A. normal Blue-wing song (top) compared with the same song in which the B phrase has been artificially segmented to resemble Golden-wing patterning (exp. 11). B. songs with normal Blue-wing A phrase (top) and normal Golden-wing A phrase coupled with Clay-colored Sparrow endings that were used in exp. 12 .

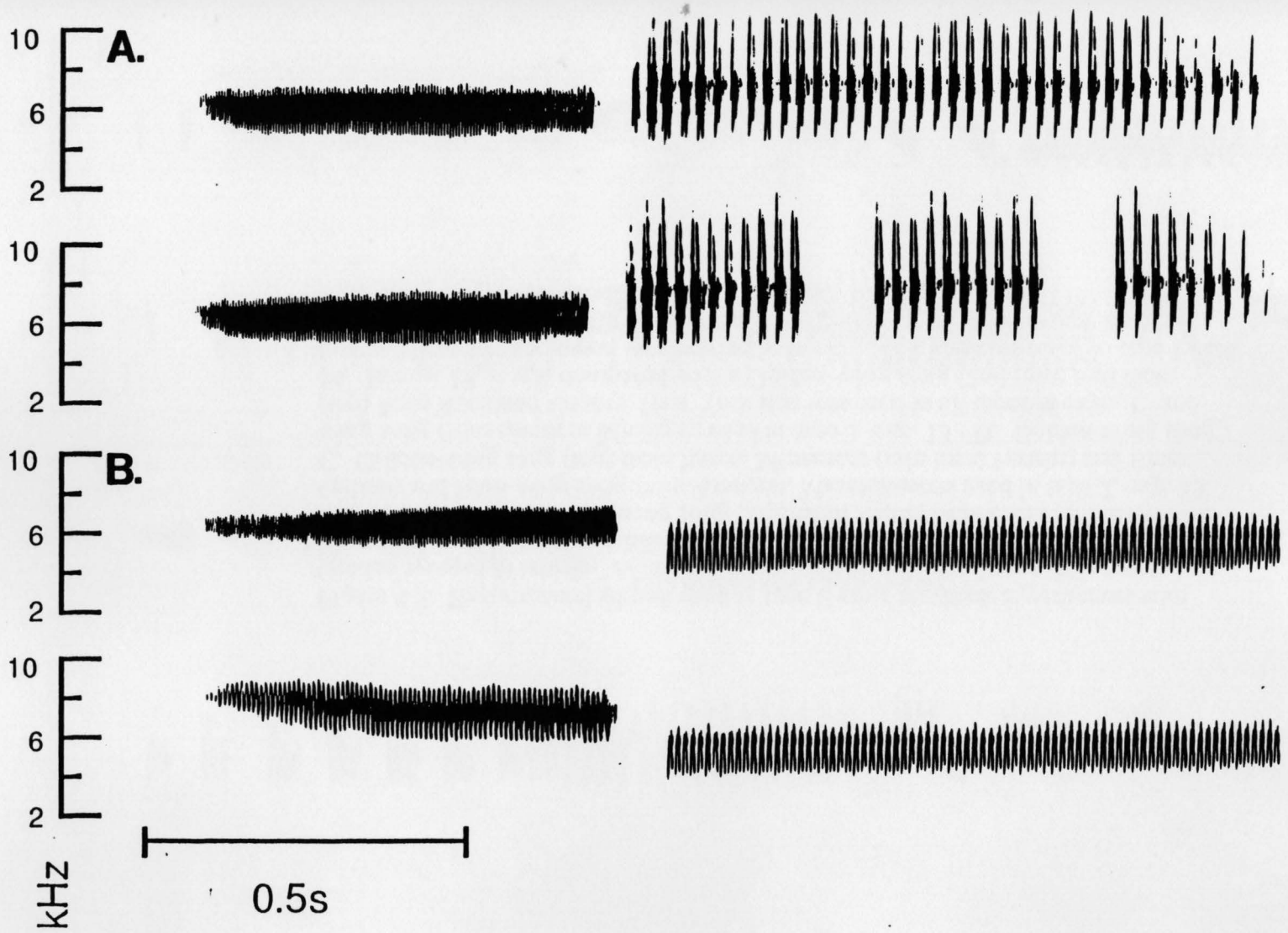
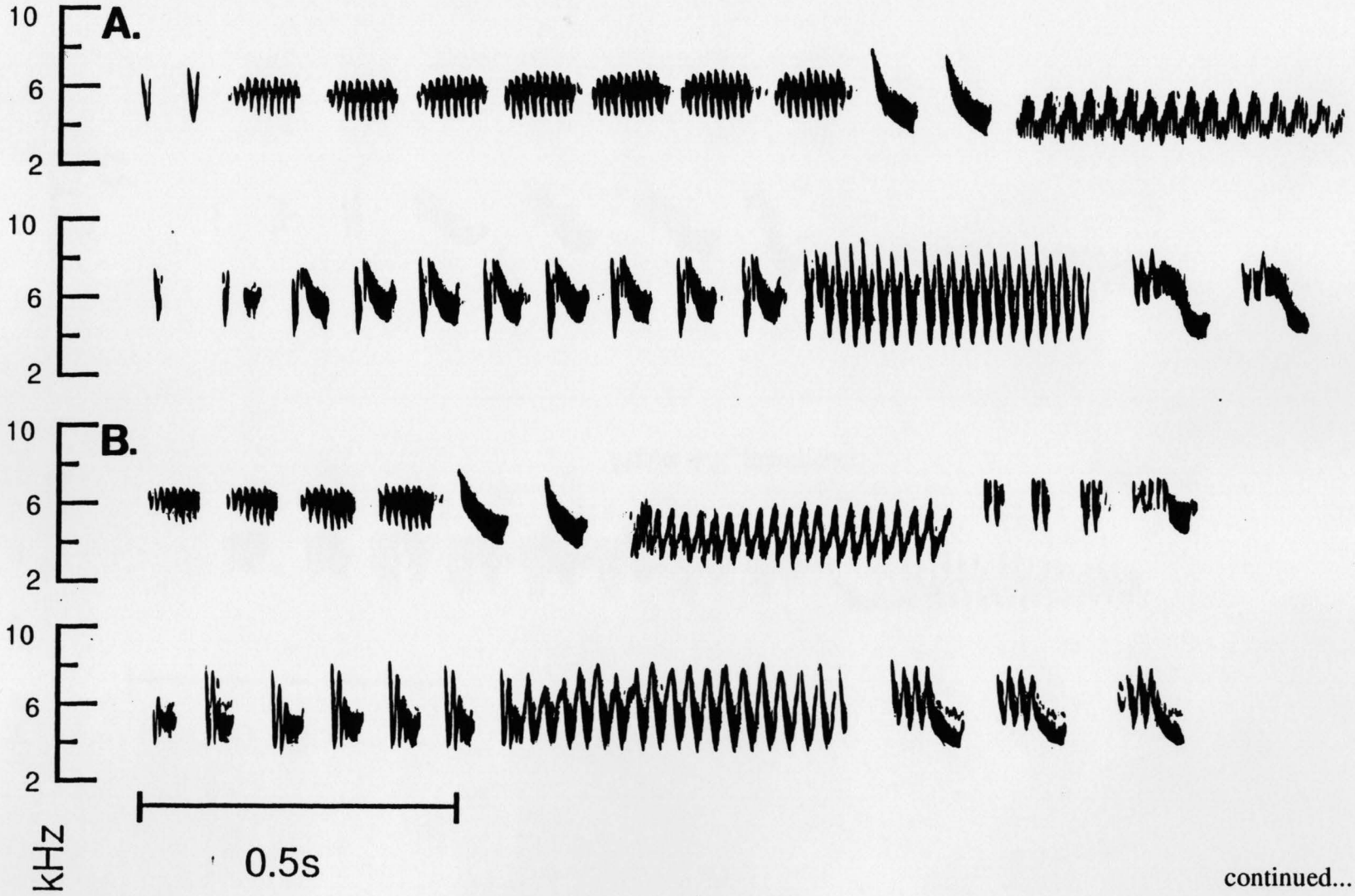
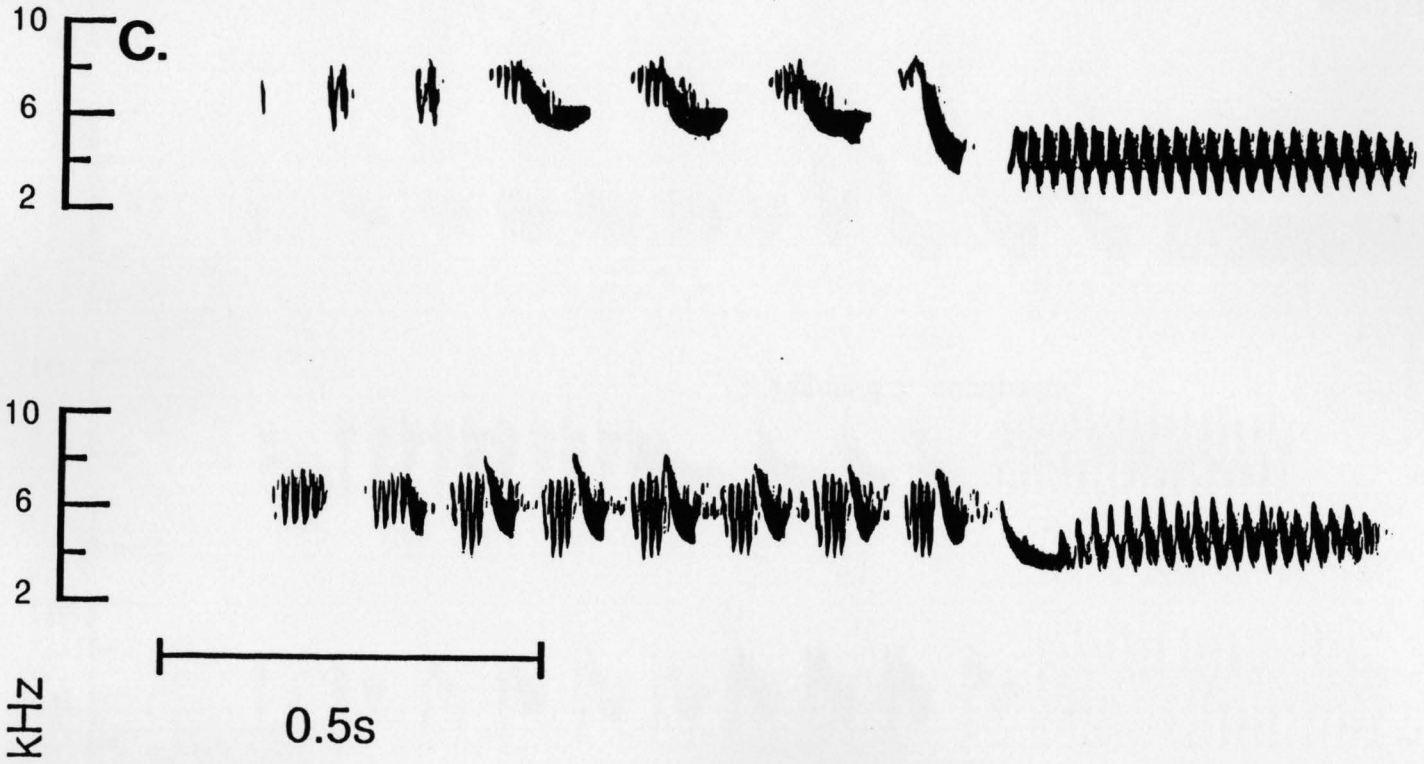

A.
B.
10
6
2
kHz
0.5s

Figure 4.5. Experimental stimuli used in type II song playback experiments with Golden-winged Warblers. A. Golden-wing song (top) from Itasca, Minnesota (common local variant) and Blue-wing song from Brookfield, Massachusetts used in tape 1, exp. 13. B. Golden-wing song (top) from Itasca, Minnesota (common local variant) and Blue-wing song from Amherst, Massachusetts used in tape 2, exp. 13. C. Golden-wing song (top) from Itasca, Minnesota (rare local variant) and Blue-wing song from southern Michigan used in tape 3, exp. 13. D. Golden-wing song (top) from Rockland County, New York that was used in all tapes in exps. 13 and 14. In exp. 13, it was compared with a Golden-wing song (2nd from top) from Itasca, Minnesota (common local variant). In exp. 14, it was compared in tape 1 with a Blue-wing song from Millbrook, New York (3rd from top) and in tape 2 with a Blue-wing song from Brookfield, Massachusetts (bottom).



continued...

Figure 4.5. continued.



continued...

Figure 4.5. continued.

D.
10
6
2
kHz
0.5s

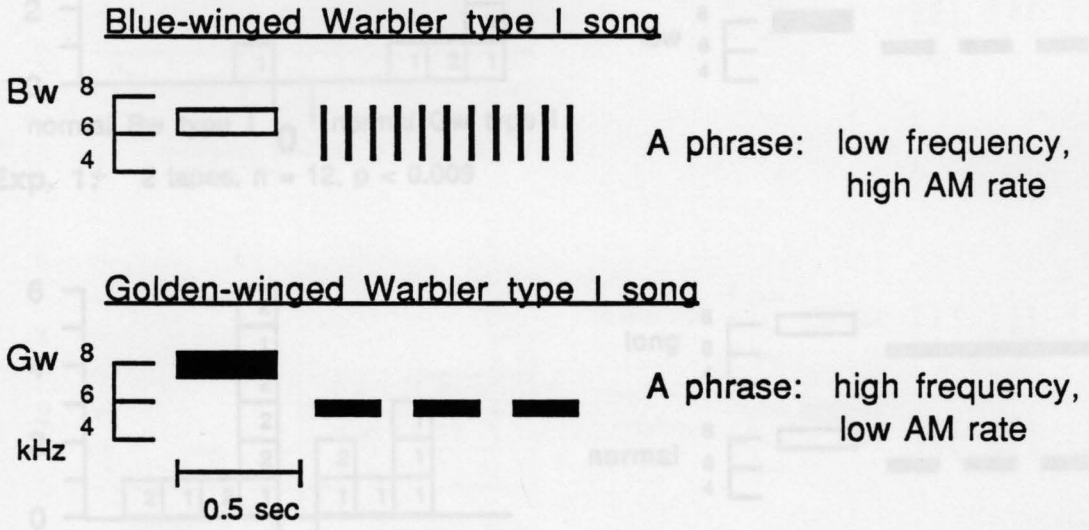
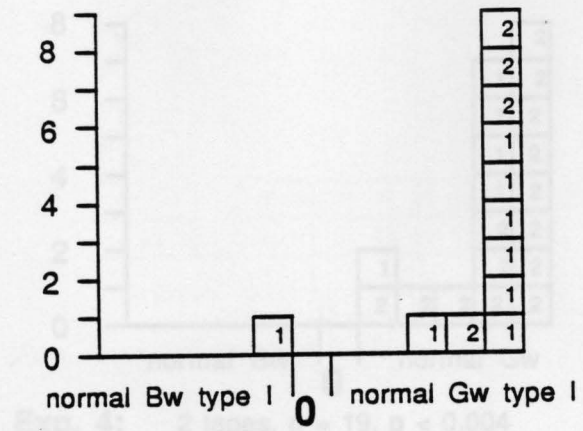
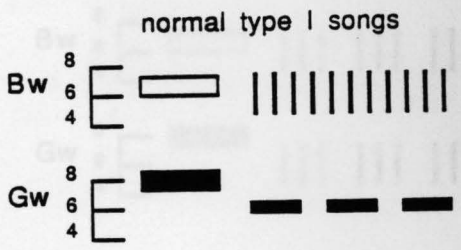
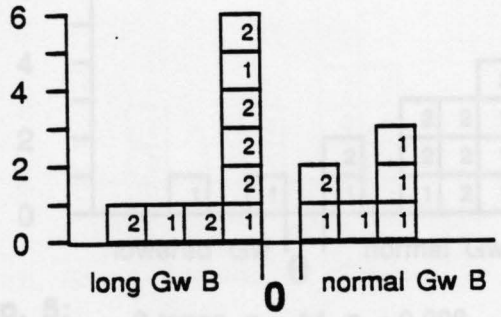


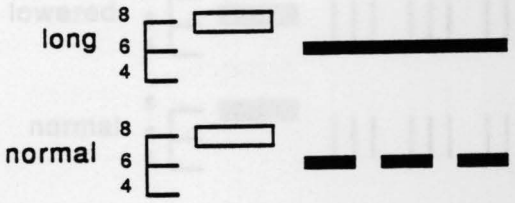
Figure 4.6. Schematic representation of normal Blue-winged and Golden-winged Warbler type I songs. In this and all following schematics, Blue-wing A phrases are open and Golden-wing A phrases are solid.



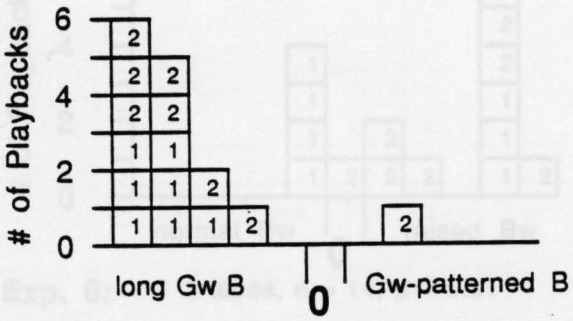


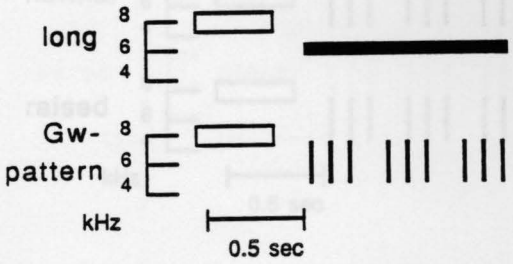
Exp. 1: 2 tapes, n = 12, $p < 0.009$





Exp. 2: 2 tapes, n = 15, $p > 0.1$

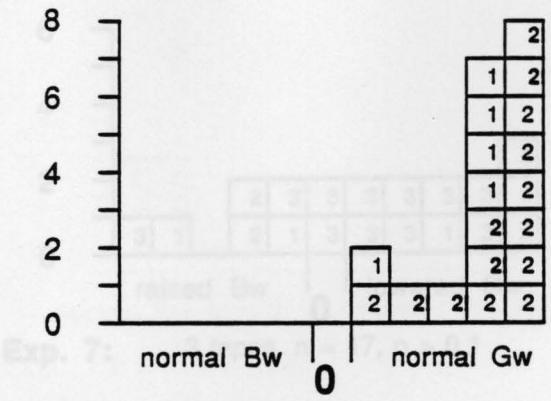




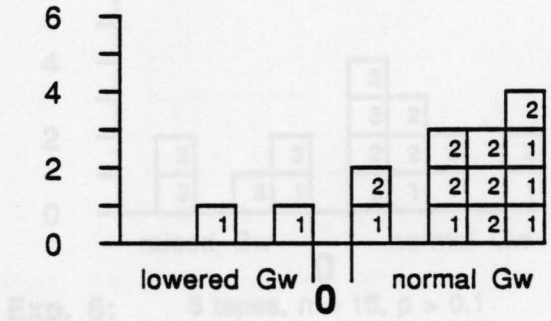
Exp. 3: 2 tapes, n = 15, $p < 0.008$

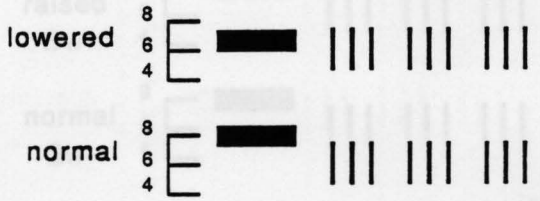
Distance

Figure 4.7. Natural type I song and song pattern comparisons with Golden-winged Warblers. Results of playback experiments are presented as described in Figure 4.2. Probability values in this and all following figures were determined using the Wilcoxon matched-pairs signed-ranks test.

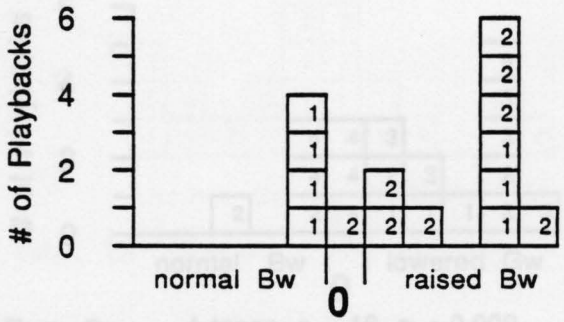


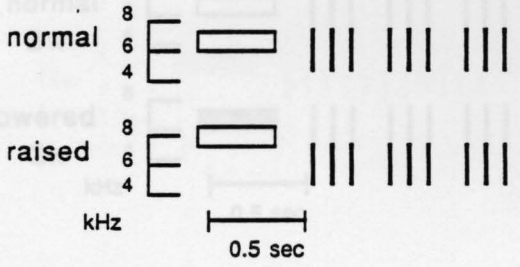
Exp. 4: 2 tapes, n = 19, p < 0.004





Exp. 5: 2 tapes, n = 14, p < 0.008

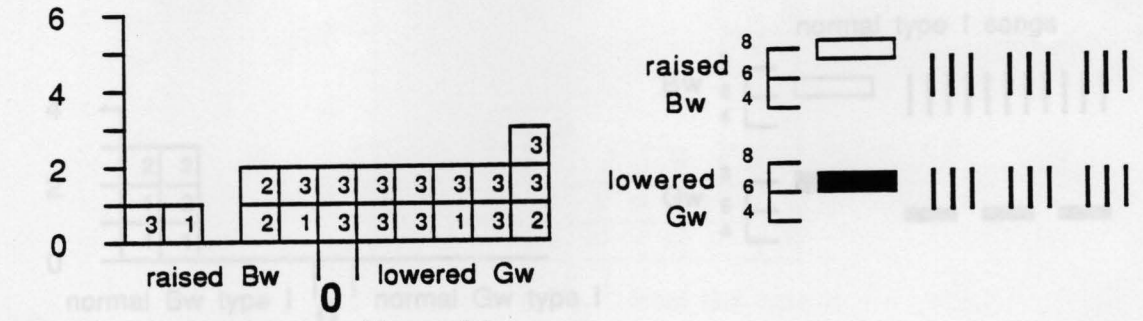




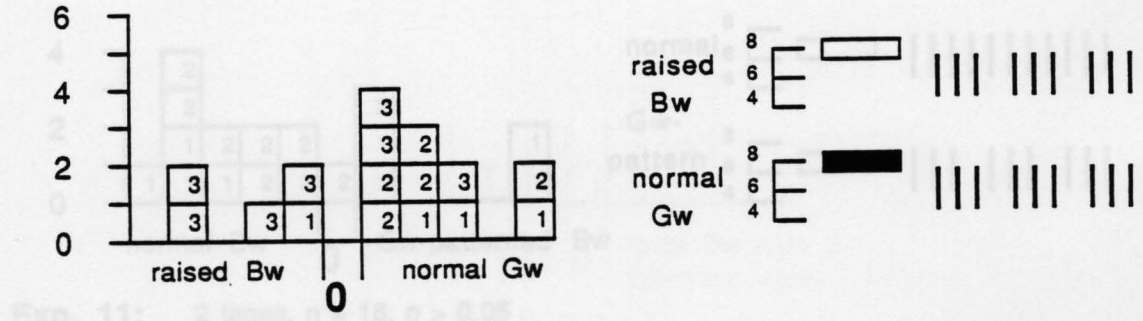
Exp. 6: 2 tapes, n = 14, p < 0.01

Distance

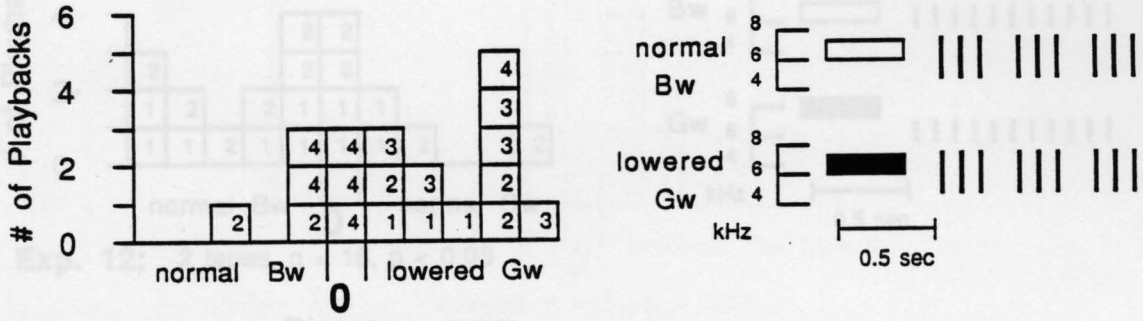
Figure 4.8. Type I song A phrase comparisons with Golden-winged Warblers. The boldface type in experiment 4 represents the single digitized tape used in that experiment.



Exp. 7: 3 tapes, n = 17, p > 0.1



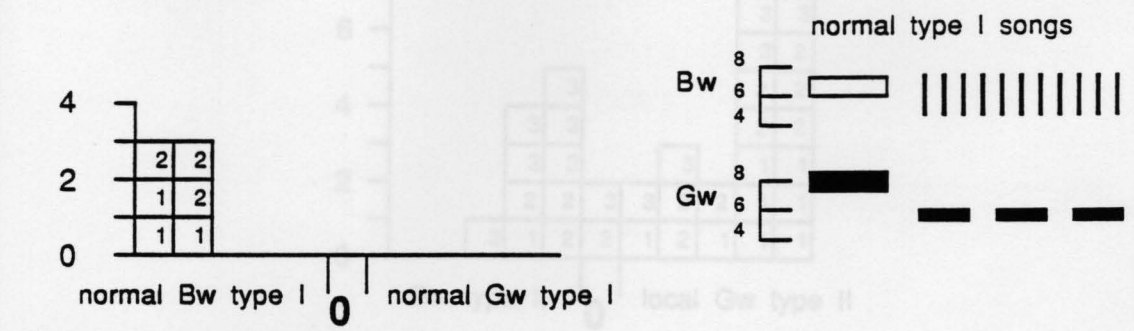
Exp. 8: 3 tapes, n = 16, p > 0.1



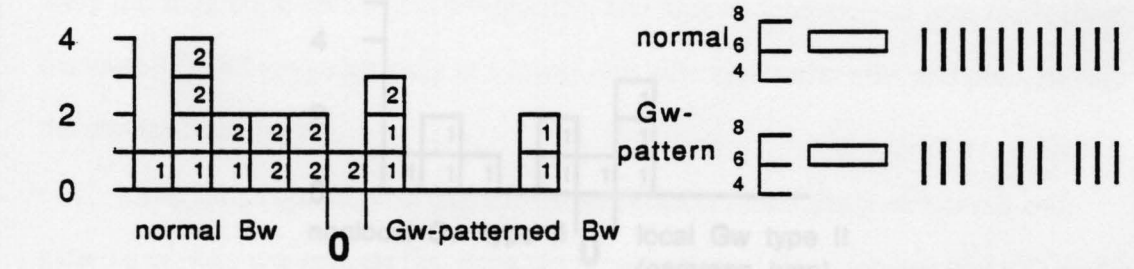
Exp. 9: 4 tapes, n = 16, p < 0.009

Distance

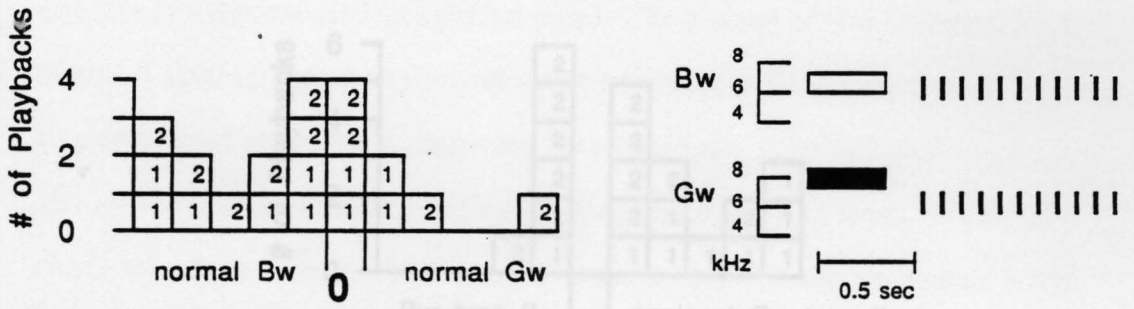
Figure 4.9. Type I song A phrase comparisons with Golden-winged Warblers.



Exp. 10: 2 tapes, n = 6



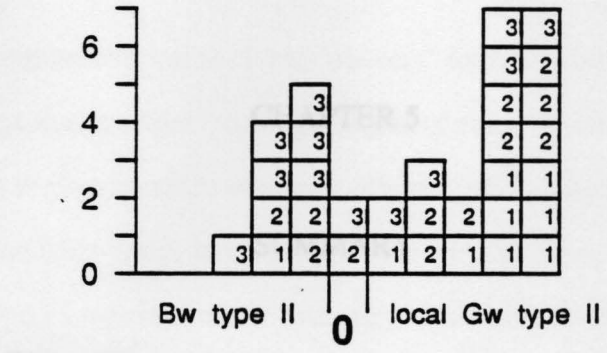
Exp. 11: 2 tapes, n = 16, p > 0.05



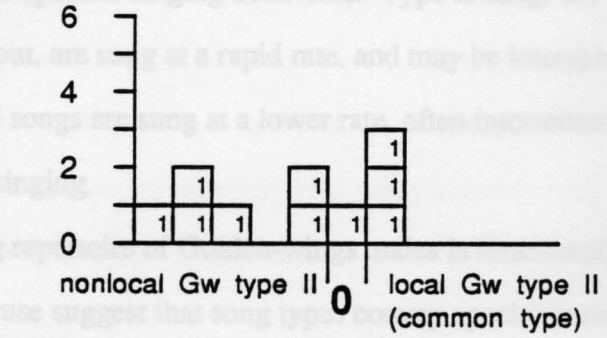
Exp. 12: 2 tapes, n = 16, p < 0.05

Distance

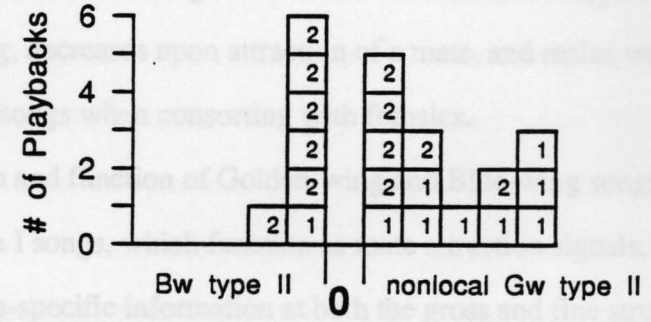
Figure 4.10. Type I song experiments with Blue-winged Warblers at Amherst, Massachusetts.



Exp. 13: 3 tapes, n = 31, p < 0.009



Exp. 14: 1 tape, n = 9



Exp. 15: 2 tapes, n = 21, p > 0.05

Figure 4.11. Type II song playback experiments with Golden-winged Warblers at Itasca, Minnesota.

CHAPTER 5

SUMMARY

The vocal behavior of Golden-wing males is organized around the association of song types and specific singing behaviors. Type II songs are used in an extended early morning bout, are sung at a rapid rate, and may be interspersed with flight song displays. Type I songs are sung at a lower rate, often intermittently, and predominate during daytime singing.

The song repertoire of Golden-wings males is functionally structured and patterns of song use suggest that song types convey special intrasexual (type II) and intersexual (type I) messages. During agonistic encounters, long type I, short type I, and type II songs are used as a graded series. The amount of type I singing, but not of type II singing, decreases upon attraction of a mate, and males were observed to sing only type I songs when consorting with females.

The form and function of Golden-wing and Blue-wing songs are closely correlated. Type I songs, which function as mate attraction signals, contain a high degree of species-specific information at both the gross and fine structural levels, and are stereotyped both within and between populations. Type II songs, used almost exclusively in male-male interactions, display such marked geographic variation that determination of species-specific characteristics is difficult.

Interspecific hybrids of Golden-wings and Blue-wings generally sing type I songs characteristic of one of the parental species, and sing type II songs characteristic of their population of origin. The observed rarity of type I songs that exhibit a blending of species-specific features suggests that the ontogeny of type I

song is highly constrained, but the local "dialects" found for type II songs suggest that their development is subject to a high degree of cultural influence.

Contrary to classic selection theory, interactions/hybridization between Golden-wings and Blue-wings have apparently not led to exaggeration of species differences in type I songs in areas of sympatry. This may be due to a lack of substantial fitness costs resulting from interspecific interactions or to the inability of selection to keep pace with the rapid mixing of the two species. A greater variety of type II song forms was evident in sympatric populations but this phenomenon may be explained by either interspecific or intraspecific selection.

Males of both species discriminated easily between natural conspecific and heterospecific type I songs, but experiments with altered type I songs suggest that Blue-wings may be more sensitive to overall song pattern than are Golden-wings. Experiments involving comparisons between natural and frequency-altered song components suggest that Golden-wing males use aspects of the fine structure of songs (frequency and amplitude modulation of introductory phrases) in discrimination. Although the data from experiments with type II songs were not clear cut, the results may be interpreted to suggest that Golden-wing males discriminate between songs on the basis of familiarity and not on the basis of species differences.

The wide range of responses by males to experimental songs suggests that not all individuals within a species use the same set of discrimination "rules". A male's response to a particular stimulus may possibly be modulated by the effects of previous experiences with individuals that sang atypical songs or displayed a mismatch of song and species typical plumage.

APPENDIX

STUDY SITES

Although the majority of the work for this dissertation was done either in the Lake Itasca or Amherst areas, I personally visited another 15 localities in order to obtain recordings of Golden-wing and Blue-wing songs (see Fig. 3.1). I also used song samples recorded for me by others from an additional 2 locations. The following brief accounts are intended to describe which species occur at each site and the history, if any, of contact between the two species. My sample of usable recordings from each location and the year(s) in which they were recorded are given in parentheses (Gw = Golden-wing, Bw = Blue-wing, Br = Brewster's, Lw = Lawrence's).

Lake Itasca, Minnesota (27 Gw; 1984 - 87) -- My main study site for Golden-winged Warblers was Lake Itasca State Park and surrounding areas located in Clearwater and Hubbard Counties, north-central Minnesota. Except for a small and isolated population in southeastern Manitoba, the Itasca region comprises the northwestern edge of the Golden-wing's range. Although they were unknown in the area before about 1940 (Green and Jannsen 1975), Golden-wings are now common in a wide range of habitat types within the study area (5 to 30 year old logging clearcuts, power line cuts, old farm fields, and spruce-alder bogs). Blue-wings have not been reported as breeding in either Clearwater or Hubbard counties but they are sympatric with Golden-wings as little as 300 km to the southeast. I have noted only two unusual individuals in four years of field work at Itasca: a Blue-wing female who was briefly

paired with a Golden-wing male and a female hybrid that may have successfully paired with a Golden-wing male (Highsmith 1987).

Amherst, Massachusetts (17 Bw, 3 Gw, 3 Br, 1 Lw; 1987 - 88) -- My main study site for Blue-winged Warblers was the area surrounding Amherst in Hampshire County, west-central Massachusetts. This area is now almost exclusively populated by Blue-wings although Bagg and Eliot (1937) did not consider them as regular local nesters until the early 1930's. Golden-wings were considered a "rare summer resident" at that same time and are perhaps even less common today; I encountered only four widely separated Golden-wing territories although I found over 60 Blue-wings in 1987-1988. Hybrids were present but also widely spaced and uncommon; 3 "Brewster's" and one "Lawrence's" were discovered during the two field seasons. Birds were present almost exclusively in power line cuts and in old farm fields.

Mille Lacs Wildlife Management Area, Minnesota (9 Gw; 1987) -- A dense population of Golden-wings was found in this large checkerboard of old to recently logged tracts just south of Mille Lacs Lake in Mille Lacs County, east-central Minnesota. Although Blue-wings and Golden-wings are sympatric as little as 50 km to the southeast, Blue-wings have not been reported as nesting in this area.

Murphy-Hanrehan Park Reserve, Minnesota (6 Bw; 1987) -- Among the many Blue-wings resident in open woodland in this area just south of Minneapolis (Scott County), I found a single normally plumaged male who sang a Golden-wing type I song. The most recent nesting of a Golden-wing in the southern part of the state was at this site in 1985 when a male Golden-wing paired with a female "Brewster's" (Jannsen 1987).

Luttchen Woods, Minnesota (3 Bw; 1987) -- Only Blue-wings were present as breeders at this site near Reno (Houston County) in extreme southeastern Minnesota. Birds were recorded for me at this site by Bill Evans.

Pellston, Michigan (8 Gw; 1987) -- Only Golden-wings were present at this location at the tip of Michigan's lower penninsula (Emmet County). Birds were common only in one 5 - 15 year old clearcut and were otherwise scattered along back roads in open deciduous woodlands.

Hope, Michigan (7 Gw, 4 Bw; 1987) -- Both Golden-wings and Blue-wings were present in abandoned agricultural fields at this location just north of the city of Midland (Midland County). The area lies close to the northern limit of the Blue-wing range in Michigan and Blue-wings have been present as a breeding species only for the last decade or so (Will 1986). Both species are regularly found in the same fields and territories frequently overlap.

Caro, Michigan (6 Gw, 3 Bw, 1 Br; 1987) -- This area in east-central Michigan (Tuscola County) is much like that around Hope but the overlap of the two species has a longer history and hybrids have been found in the last few years (T. Will pers. comm.). As at Hope, Golden-wing and Blue-wing territories may be adjacent and/or overlap.

Chelsea, Michigan (8 Bw, 1 Br; 1987) -- This area of abandoned farmland in southeastern Michigan (Washtenaw County) was reported to me to have many Blue-wings and a few Golden-wings (T. Will pers. comm.), but I found only Blue-wings and a single "Brewster's" hybrid.

Gravenhurst, Ontario (8 Gw; 1987) -- Only Golden-wings were present as a nesting species at this area near the northern edge of their range (Muskoka County), although an unmated Blue-wing (only the second sighting in 15 years) spent much of the season on a territory in marginal habitat (B. Bowles pers. comm.).

Halton Regional Park, Ontario (6 Gw, 1 Bw; 1987) -- I found a single Blue-wing in an old field with several Golden-wings and more Golden-wings were nearby in a cedar swamp at this location just north of Campbellville (Halton County). Hybrids were present in the 1960's (R. D. James pers. comm.) but I have no more recent information.

Audley, Ontario (1 Bw, 1 Br; 1987) -- I located only a single Blue-wing and a "Brewster's" at this site in abandoned farmland about 20 km east of Toronto (Halton County).

Ithaca, New York (4 Bw, 2 Br; 1987) -- The Connecticutt Hill Wildlife Management Area, a few kilometers southeast of Ithaca, New York (Tompkins County), has a long history of hybridization between Golden-wings and Blue-wings (Short 1963, Ficken and Ficken 1968) but only Blue-wings and two "Brewster's" hybrids were found in 1987 by Bill Evans.

Rutland, Vermont (1 Gw, 1 Bw, 2 Br; 1987) -- I found one Blue-wing, one Golden-wing, and two "Brewster's" in old fields near a rest stop off Route 4 about 25 km west of Rutland. The area has had a mixture of species and hybrids for several years (N. Martin pers. comm.).

Pleasant Valley Audubon Sanctuary, Massachusetts (1 Gw, 2 Bw; 1987) -- Two Blue-wings and a Golden-wing were present at this small area of old pasture near Lenox (Berkshire County).

Newbury, Massachusetts (2 Bw; 1987) -- Many Blue-wings were found in an old field on Pyke's Bridge Rd. several km west of Newbury (Essex County). Golden-wings have occasionally been found in this area in the last decade.

LaSallette State Park, Massachusetts (1 Gw, 2 Bw; 1987) -- A single Golden-wing and several Blue-wings were found in marginal habitat near this site in Topsfield (Essex County).

Oak Ridge, Tennessee (3 Gw; 1987) -- Three Golden-wings were recorded for me by Don Kroodsma in a mountainous area (American Knob, Anderson County) where Blue-wings are unknown as a breeding species (R. Kroodsma pers. comm.).

Columbia, Missouri (1 Gw, 8 Bw; 1988) -- Blue-wings are local in old fields at this site near the southwestern edge of the species' range in central Missouri (Boone and Callaway Counties). Although the area is many hundreds of kilometers from what is considered to be the normal range of Golden-wings (Will 1986), I found a single territorial Golden-wing male among a cluster of Blue-wings. Golden-wings are typically seen only occasionally in migration through this region (T. Barksdale pers. comm.).

Greer, Missouri (5 Bw; 1988) -- I found only Blue-wings in recently thinned woodlands in this region near the southern limit of the species' range in southern Missouri (Oregon and Shannon Counties).

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